USING MOVEMENT ECOLOGY TO UNDERSTAND FLIGHT BEHAVIOR IN SOARING BIRDS

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Understanding the process by which animals make decisions based on cues in their environment is a central challenge in behavioral ecology. We focus here on the process by which soaring migrant birds use landscape and weather features to make decisions during various aspects of flight. We examined how Tree Swallows weigh safety against speed in obstacle-avoidance trials; how Turkey Vultures use artificial thermals to extend foraging past dusk; the movement ecology of migration in Turkey Vultures, including energetics, route choice, and use of surface features, turbulence, and winds; how migrating vultures vary in their use of these features according to whether they live in mountainous, flat, coastal, or inland environments; and how vultures vary in their use of weather features according to the time of year, and whether they are breeding, over-wintering, or migrating. To examine these questions, we employed a variety of experimental, computational, and statistical techniques. Birds were released in flight tunnels for obstacle avoidance trials, while vultures were implanted with heart rate loggers and tracked via satellite-based GPS to study movements. Weather variables were drawn from the North American Regional Reanalysis, a regional-scale meteorological model. In obstacle avoidance trials, we found no evidence that swallows exhibit side-bias to promote quick decision making. We found that,

in nature, Turkey Vultures will forage past their normal daily activity period when presented with both an artificial food source and an artificial thermal, in the form of a methane-vent. A heart rate analysis of a migrating turkey vulture suggests that the act of migration is not energetically costly for soaring migrants. An analysis of movement paths in relation to turbulence, horizontal winds, terrain ruggedness, and other descriptors such as heat flux and boundary layer height shows that movement and navigation correlates with a variety of external factors, most notably turbulent kinetic energy, horizontal winds, and surface ruggedness. We found that the way in which vultures use weather features depends on the time of year, biological motivation, the presence of mountain ranges, and the way in which these variables interact with each other.

BIOGRAPHICAL SKETCH

James Todd Mandel was born and raised in Corona del Mar, California. He attended Princeton University from 1998-2002, where he majored in Ecology and Evolutionary Biology. His undergraduate thesis explored the life-history of a large, long-lived, yet ultimately suicidal, tropical tree, *Tachigalia versacolor*. While at Princeton, James had the opportunity to work, study and research in the tropics, both in Belize and Panama. After graduation, this work lead to a job in Panama, where he was the first Systems Manager for the Automated RadioTelemetry System on Barro Colorado Island, Panama. It was during this job that James first became acquainted with the massive soaring migrations that funnel through Central America every fall, and resolved to study how such a long-distance, unpowered flight took place. Excited about this project, James applied to Cornell University to explore this question as a doctoral dissertation, which is what you're now reading, 6 years later. After finishing his dissertation, James will work for McKinsey and Company as a consultant, and will continue working with Advanced Conservation Strategies, a non-profit environmental consultancy and research agency, on market-based approaches to environmental problems. James lives in Philadephia, PA with his wife, Abigail.

I’d like to dedicate this work to my wife, Abby, my supportive family and friends, Hawk Mountain (and all the other small, nature and science loving community organizations like it), and to all of the birds who decided to feed on a slightly suspicious carcass and ended up with a scary story to tell their bird friends, with the wing tags to prove it.

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Introduction

Ecology has been defined as "the science by which we study how organisms interact in and with the natural world".[1] The study of movement is central to this challenge, since it is critical to understanding the spatial distributions of organisms and how they respond to changes in their environment. Individual models of animal movement within the natural environment have accelerated with advances in computational strength and remote sensing. Specifically within bird flight, there is an abundance of data on movement patterns, which have been growing since the advent of bird banding in 1899.[2] Furthermore, scientific banding has been augmented by individual telemetry.[3] This combination of banding and tracking has lead to the recognition of a diversity of patterns of bird movement, and spawned a body of theory in underlying movement process. It is fairly common to see in the scientific literature studies on movement patterns in birds, and a wealth of papers on "optimal movements" [4,5] for behaviors like foraging, predator avoidance, and migration. Within this optimality literature, several variables have been suggested for optimization; chief among these is time-minimization and energy-minimization. When to use different optimality criteria, and how to relate these optimalities to broad patterns of movement, is a challenging problem, but a critical one to understanding how birds move. Some of the

[1] Ricklefs RE (1996). The economy of nature. WH Freeman and Company. New York.
[2] Spencer R (1985). Marking. In Campbell B, Lack E (eds) A dictionary of birds. British Ornithologists' Union. London. pp 338-341.
[3] Cochran WW, Lord RD (1963). A radio-tracking system for wild animals. *J Wildlife Manag*. 27:9-24.
[4] Pennycuick CJ (1989). Bird flight performance. A practical calculation manual. Oxford University Press. Oxford.
[5] Hedenstrom A, Alerstam T (1995). Optimal flight speed of birds. *Phil Trans Roy Soc B*. 348:471-487.

challenges in this effort are 1) addressing the large scale of movements in organisms that routinely cross continents, 2) developing estimates of internal and external states of the animals that are sufficiently standardized to apply across all of the scales relevant to the animal, and 3) developing appropriate methodologies to relate differences in movement to changes in state, and then relating this back to fundamental theory.

In this dissertation, I relate movement patterns to external conditions across a range of scales, geographies, and biological motivations, and use these relationships to infer underlying movement processes. It is my hope that understanding the relationship between process and pattern will ultimately help inform the underlying models that give us our understanding of how and why birds move.

In the first chapter, I explore the relevance of optimal movement theory in obstacle-avoidance behavior during flight in tree swallows. In predator or obstacle avoidance, optimal movement suggests that time-minimization should be the dominant criterion. In many species, this leads to movement handedness; an organism has pre-programmed avoidance direction and movement behavior. However, there is an implied trade-off between response time and predictability of movement, such that animals must be both fast and unpredictable to avoid capture. Many species have solved this challenge through density-dependent “handedness”. In a population, all organisms have a preferred direction, but for a minority of these individuals, the direction is the exact opposite of the majority. Even though every individual will always avoid in the same way, a predator will not know which direction this is. In flight, aerial predation and obstacle avoidance is quite common, and the need for quick responses is enhanced by the high speeds of flight. However, the complexity

of maintaining stable flight, and the need for symmetrical musculature for energy minimization, implies that there is a trade-off within the individual. Using an experimental design within a flight tunnel, we tested this trade-off and found that the solution of handedness does not seem to apply for birds that fly most of their waking hours.

The second chapter presents the results of an observational study in which another soaring bird, the turkey vulture, employs a novel behavior to overcome a natural ecological constraint. Turkey vultures are commonly known to be “late risers”, to go to roost when thermals dissipate, and be strongly obligate thermal soaring birds. As a result, they are strongly diurnal, with a relatively restricted activity period. Given that they can get plenty of food in a short amount of time from a single carcass, this is generally not a problem. However, anthropogenic changes in the environment can cause novel challenges: at garbage dumps and landfills, food is both abundant and consistent, but so is competition. Vultures seem to spend much more energy competing over food, and some of them ultimately seem to spend much longer times waiting for access to carcasses. This puts pressure on vultures to extend their daily foraging past the periods when natural thermals are readily available for easy flight. The observed “solution”, for birds to start using methane vents as artificial thermals to fly efficiently at night, yields a host of interesting questions about pattern and process in soaring flight. It reveals a behavioral plasticity that is somewhat surprising, as well as suggesting that atmospheric dynamics restrict, and likely determine, movement in this species.

This indication that turkey vultures are both behaviorally plastic and that atmospheric dynamics are likely a key determinant of movement makes them an ideal species for studying how movement process leads to a diversity of

movement patterns. They are the only vulture that makes long-distance, intercontinental migrations and they span a behavioral range from non-migrant through partial migration to long-distance obligate migration. In addition to being an appropriate species behaviorally, the availability of detailed and standardized databases of a large variety of weather phenomena and the ability to collect detailed movement trajectories using GPS technology made such a study feasible. In chapter 3, I set out to create a detailed description of the movement processes that underlie long-distance soaring migration within a movement ecology framework. We were able to capture the key dynamics of both movement and navigation, which relied in large part on the interactions of turbulence regimes, surface heterogeneity, and horizontal winds. Implanted heart rate sensors showed little change in energy expenditure as a function of distance, suggesting that birds do not spend more energy to go longer distances in a set amount of time. Combined with observations that show extremely low flapping rates, this suggests that energy-minimization plays a role during fall migration.

The models developed for chapter 3 created an excellent basis for asking some fundamental ecological questions. In chapter 4, I extend this initial description of migration to see how well it supports predictions of migration over varying geography and of different migratory intensity. Sampling vultures from three locations that varied in terrain ruggedness and migratory intensity (one mountainous long-distance migrant, one mountainous short-distance migrant, and one long-distance plains migrant), I applied the same movement ecology model to see how vultures handled the challenge presented by weather. I found that migratory intensity did not predict the use of weather nearly as much as did terrain type. The results suggest the existence of two

distinct migratory systems: the migrants that lived near mountains used both slope-soaring and thermal soaring, while the plains migrants relied solely on thermal-soaring. The key to this difference was encapsulated in their opposite response to horizontal winds. Using the navigational component of the movement ecology model, I saw that migrants in hilly terrain changed course in a way that optimized the use of slope-soaring with horizontal winds, while plains migrants reduced distances and compensated for wind-drift. The birds in hilly terrain had altered their movement and navigational styles to use their surroundings most efficiently.

The two studies of fall migration in turkey vultures revealed a variety of strategies based on surroundings, all broadly falling within the context of energy minimization: thermal turbulence is relied upon and slope-soaring is used when mountains are available. Birds adjust their path differently depending on the availability of rugged terrain for slope-soaring. It is not clear, however, that energy-minimization should apply year round. In chapter 5, I applied movement ecology models to the rest of the annual cycle: spring migration, breeding period, and wintering periods. I found a signature of time-minimization during spring migration: birds engage less in slope-soaring, and increase their activity period. On the breeding grounds, energy minimization appears not to apply at all. During this period, birds do not alter their course for any weather or terrain phenomena. It is likely that, during this food rich but energetically demanding period, they focus on providing food to young without regard to route optimization.

This dissertation lays a foundation for advancing studies of movement by incorporating weather and landscape models that are standard tools in meteorological studies of climate change, and that, for the first time, allow

comparisons of flight conditions between birds across a continental scale. Understanding how movement decisions relate to a birds environment allows for a deeper understanding of the process by which animals move; connecting these relationships between environment and movement with regional scale models that are used in forecasting should allow us to generate predictions about how soaring flight patterns might change as atmospheric conditions change.

CHAPTER 1

LATERALITY AND FLIGHT: CONCURRENT TESTS OF SIDE-BIAS AND OPTIMALITY IN FLYING TREE SWALLOWS

Mandel JT, Ratcliffe JM, Cerasale DJ, Winkler DW (2008).
Laterality and flight: concurrent tests of side-bias and optimality in flying tree swallows. *PLoS ONE* 3(3): e1748.

Abstract

Behavioural side-bias is a result of hemispheric specialization and is advantageous because it can improve response times to sudden stimuli and efficiency in multi-tasking. It has been observed in many vertebrates, including birds. However, behavioural side-bias can lead to morphological asymmetries resulting in reduced performance for specific activities. For flying animals, wing asymmetry is particularly costly and it is unclear if behavioural side-biases will be expressed in flight; the benefits of quick response time afforded by side-biases must be balanced against the costs of less efficient flight due to the morphological asymmetry side-biases may incur. Thus, competing constraints could lead to context-dependent expression or suppression of side-bias in flight. In repeated flight trials through an outdoor tunnel with obstacles, tree swallows (*Tachycineta bicolor*) preferred larger openings, but we did not detect either individual or population-level side-biases. Thus, while observed behavioural side-biases during substrate-foraging and copulation are common in birds, we did not see such side-bias expressed in obstacle avoidance behaviour in flight. This finding highlights the importance of behavioural context for investigations of side-bias and hemispheric laterality and suggests

both proximate and ultimate trade-offs between species-specific cognitive ecology and flight biomechanics.

Introduction

Hemispheric specialization, the division of neural processing tasks between the left and right hemispheres of the brain, is generally agreed to be responsible for sensoribehavioral side-biases in reptiles, birds, and mammals (Rogers, 2000; Rogers, 2002; Vallortigara, 2006). Hemispheric specialization and resultant perceptual side biases may provide animals with a hard-wired rubric for life-preserving decisions. One hypothesis suggests that lateralization of cognitive and visual processing minimizes response time (e.g., light-exposed chicks, *Gallus gallus domesticus*, always use the left eye for predator recognition when given a choice, and show longer habituation times to visual patterns when forced to use the right eye; Rogers, 2000; Dharmaretnam and Rogers, 2005). In three species of toads (*Bufo* spp.) side-bias is expressed when individuals are confronted with predators; escape responses are faster when predator models are introduced from their left side than from the right, and the type of response (sideways vs. forward jumps) varies with side of presentation (Lippolis *et al.*, 2002). Hemispheric specialization, and associated perceptual biases and asymmetrical motor responses, appears to be highly conserved in vertebrates (Vallortigara and Rogers, 2005; Robins and Rogers, 2006).

In birds, chicks (Dharmaretnam and Rogers, 2005; Vallortigara *et al.*, 1996; Deng and Rogers, 1997), pigeons, *Columba livia* (Deng and Rogers, 1997; Prior *et al.*, 2002; Prior *et al.*, 2004), and black-winged stilts, *Himantopus himantopus* (Ventolini *et al.*, 2005), have been shown to favour one

hemisphere over the other for making specific decisions. Whatever the underlying mechanisms, brain lateralization is positively correlated with efficient neural processing and multitasking (Rogers, 2000; Vallortigara, 2006; Rogers *et al.*, 2004). Selection for such decision-making should lead to quicker response times, and might explain the apparent ubiquity of hemispheric specialization and side-bias in vertebrates (Ventolini *et al.*, 2005; Rogers *et al.*, 2004).

However, there are putative disadvantages to lateralization; stereotypical behaviours are by definition easily predicted. Prey with perceptual side-biases should exhibit slower response times to attacks coming from one side versus the other, and such a weakness may well be exploited by predators (Rogers, 2002; Lippolis *et al.*, 2002; Ventolini *et al.*, 2005). Behavioural side-bias can also cause developmental asymmetries in the skeleton and musculature (Adam *et al.*, 1998). For fast-flying birds, wing asymmetry will reduce flight performance (Thomas, 1993; Moller and Swaddle, 1997; Swaddle and Witter, 1997), increase predation-risk (Moller and Nielsen, 1997), and negatively impact fitness (Birkhead and Moller, 1992). Asymmetrical musculature could likewise be assumed to negatively affect flight performance. Assuming cognitive systems can drive the evolution of behaviours (Dukas, 2004), selection should act to reduce the expression of behavioural side-bias when consequences are disadvantageous (Vallortigara and Rogers, 2005), such as when it will lead to wing or muscular asymmetry. Thus, a behavioural side-bias may be expressed when advantageous and masked when not.

Here, we examine laterality and the expression of side-bias in the broader context of competing constraints. We do this using an aerial hawking, insectivorous bird: the tree swallow, *Tachycineta bicolor*. This species exhibits

behavioural side biases in copulatory behaviour on the ground (Peterson *et al.*, 2001) and strong stabilizing selection has been suggested to preserve wing symmetry (Balmford *et al.*, 1993; Brown and Bomberger-Brown, 1998).

We implement an experimental design in which a bird escapes through a tunnel containing an obstacle varying in size and position. Because fast response times should be favoured during escape, we expected behavioural side-bias might be expressed under our experimental conditions for obstacle-avoidance behaviour. However, given the potential cost of behavioural side-bias in wing and muscular asymmetry (and reduced overall flight performance), we also expected behavioral side-biases might instead be masked. To our knowledge, this is the first study to consider the potential conflict between selection for wing symmetry and selection for side-bias in flying birds.

Materials and Methods

(a) Birds, field site and flight tunnel

Experiments were conducted at the Cornell University Experimental Ponds Facility in Ithaca, New York, U. S. A. (42° 30’ N, 76° 28’ W). Twenty-four female tree swallows were captured from their nest boxes during incubation between 24 May and 31 May 2006. Birds were aged by plumage (Pyle, 1987), and right and left tarsi and flattened wing lengths were measured (+-0.1 mm). During experiments (see below), birds were released individually into an outdoor plywood flight tunnel (1.22 * 1.22 * 9.75 m long) from a lightproof box centred on top of the southwest end. The walls and ceiling of the tunnel were painted matte white and the floor covered with white limestone pebbles in an effort to minimize unintended perceptual asymmetries. The tunnel was

illuminated by ten lights distributed equally along the two long walls (for further details of tunnel and study site see Bowlin and Winkler, 2004). Within the tunnel, 3.22 m from the southwest end, the lower half (h61*w122 cm) was blocked using a light blue Styrofoam sheet (2.5 cm thick). The upper half was partially blocked using sheets 61 cm in height and of various widths (see Figure 1.1). Each bird flew through the tunnel and was caught at the end of the tunnel in a mist net a total of four times, and was then released at point of capture.

(b) Experiment 1

Twelve swallows served as subjects in experiment one. These animals did not serve as subjects in experiment two. The purpose of this experiment was to determine whether birds would demonstrate a side-bias while escaping the tunnel or, would make an optimal choice when presented with obstacles within the tunnel: in this case, a larger opening that would be easier to navigate.

First, two light blue h 61 * w 41 cm Styrofoam sections were put into place above the lower sheet flush with the sides of the tunnel, creating a h 61 * w 41 cm centred opening in the upper-half of the obstacle (Figure 1.1, trial 1). This trial was used to acclimate the bird to the tunnel. In the second trial, a single sheet was positioned such that two equal sized openings (h 61*w 41 cm) exist on either side (Figure 1.1, trial 2). The bird was released and scored as having used either the right or left opening. In the third trial, this centre section was moved 7.5 cm towards the side the bird had flown through on the previous trial (Figure 1.1, trial 3). The bird was released, scored as either having made an optimal decision (large opening (h61*w48.5 cm), opposite of side chosen in trial one) or a non-optimal decision (small opening (h61*w33.5 cm), same side

as chosen in trial one), and caught. In the fourth and last trial, the off-center upper section used in trial three was removed. A wider section (h61*w56 cm) was positioned in the opening, leaving two equal sized openings (h61*w33.5 cm) on either side (Figure 1.1, trial 4). The bird was scored as having used either the same or the opposite opening as used in trial two.

(c) Experiment 2

Twelve swallows served as subjects in experiment two. The purpose of this experiment was similar to that of the first experiment, but also controlled for a potential confounding variable in the experimental design: that a bird's preference for small or large openings might mask the test of side-bias.

Experiment two was identical to experiment one with the following exception: in the fourth and last trial, rather than use the wide section, a narrow section (h61*w33.5cm), creating two openings the size of the larger opening (h61*w48.5 cm) in trial three was used.

(d) Statistical analyses

Using the program *R* v. 2.3.1 (Ihaka and Gentleman, 1996), we ran custom randomization tests to determine if (a) the swallows exhibited a population-level side-bias by testing if the right or left side was chosen on trial two more often than expected by chance (results from two experiments pooled), (b) the optimal side was chosen by individuals more often than expected if both openings had been of equivalent size (results from two experiments pooled; trial 2 vs. trial 3), and (c) individuals exhibited a side-bias by testing if the side chosen in trial two was chosen more often than predicted by chance in trial four (tested separately between experiments). The absolute difference in wing

and tarsus length between each appendage relative to the average of both appendages was measured. Paired *t*-tests were used to compare the magnitude of asymmetry (i.e. absolute value) between tarsi and wing lengths. *G*-tests of goodness of fit were used to test for a consistent direction of asymmetry (or lack thereof) in the tarsi and wings of individual birds and to test whether such direction of asymmetry in both tarsus and wings was related to side chosen in trial 2 of experiments 1 and 2.

Results

Seven females were second year, nine were >3 years and 8 were adults (> 1 yr.) of indeterminate age. All 24 birds flew from the release box to the opposite end of the tunnel for all trials. When the repeated decisions of individual birds are examined, 13 of 24 birds chose the same side in trial 4 as they had in trial 2; both of these trials involved symmetrical openings (Figure 1.1). 23 of 24 birds chose the larger opening in trial 3, which was always placed opposite to their choice in trial 2 (Figure 1.1).

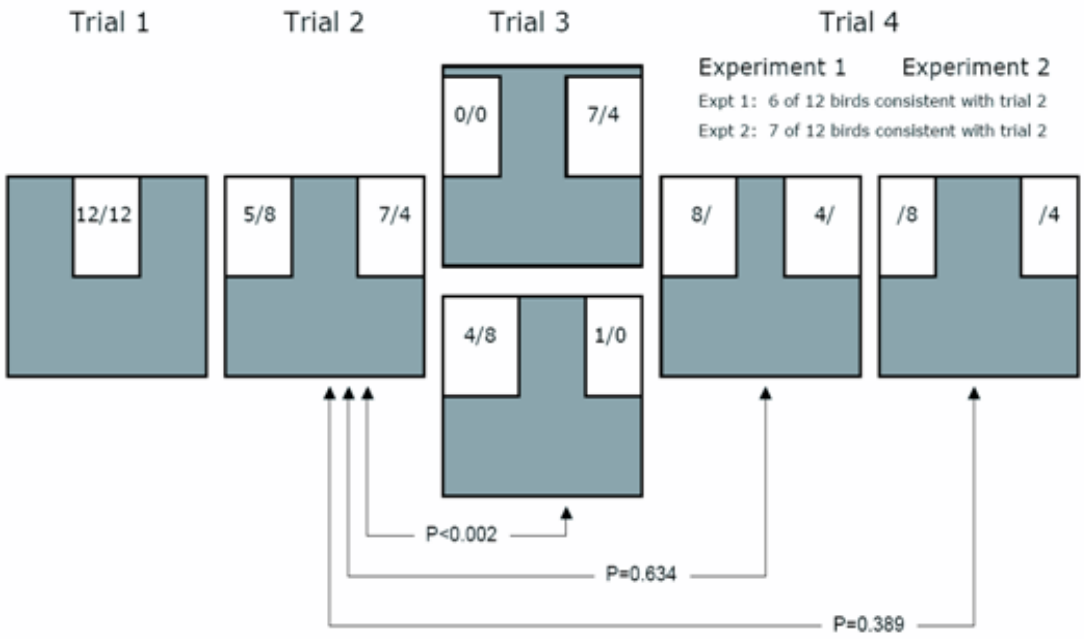

Figure 1.1. Schematic of the tunnel from the point of view of a bird entering the tunnel. Actual statistics for birds choosing a path is presented in the format x/y, where x represents the 12 birds from experiment one, and y represents the 12 birds from experiment two. In trial three, the side of the optimal choice depended on a bird's choice in trial two. To control for any initial size preference not related to optimality, half of the birds (Experiment 1) were given symmetrical, narrow openings in trial four, while half (Experiment 2) were given symmetrical, wide openings. The comparison of trial two to trial three is a test of optimality, while the comparison of trial two to trial four is a test of side-bias.

We failed to detect evidence of laterality; we found no predominance of side bias in trial two of the experiments pooled (500 permutations; actual statistic=11; $p>0.75$). The sides chosen in trials two and three were significantly different (500 permutations; actual statistic=1; $p<0.002$), indicating that the swallows chose the optimal side in almost all instances. There was also no evidence of functional asymmetry at the individual level; the side chosen between trials two and four did not differ significantly for either

experiment one (500 permutations; actual statistic=6; p=0.634) or experiment two (500 permutations; actual statistic=7; p=0.389).

Tarsus measurements exhibited significantly greater asymmetry than did wing measurements (paired *t*-test; p=0.002, Figure 1.2). We found no significant directionality at the population-level in either tarsus or wing asymmetries, and the direction of an individual's side choice in trial 2 was not related to either the direction of that same individual's asymmetry for their wings or tarsi (4 *G*-tests, p>0.3 for all). We also found no significant correlation between tarsus and wing asymmetries Pearson test (r=-.06, p=0.74).

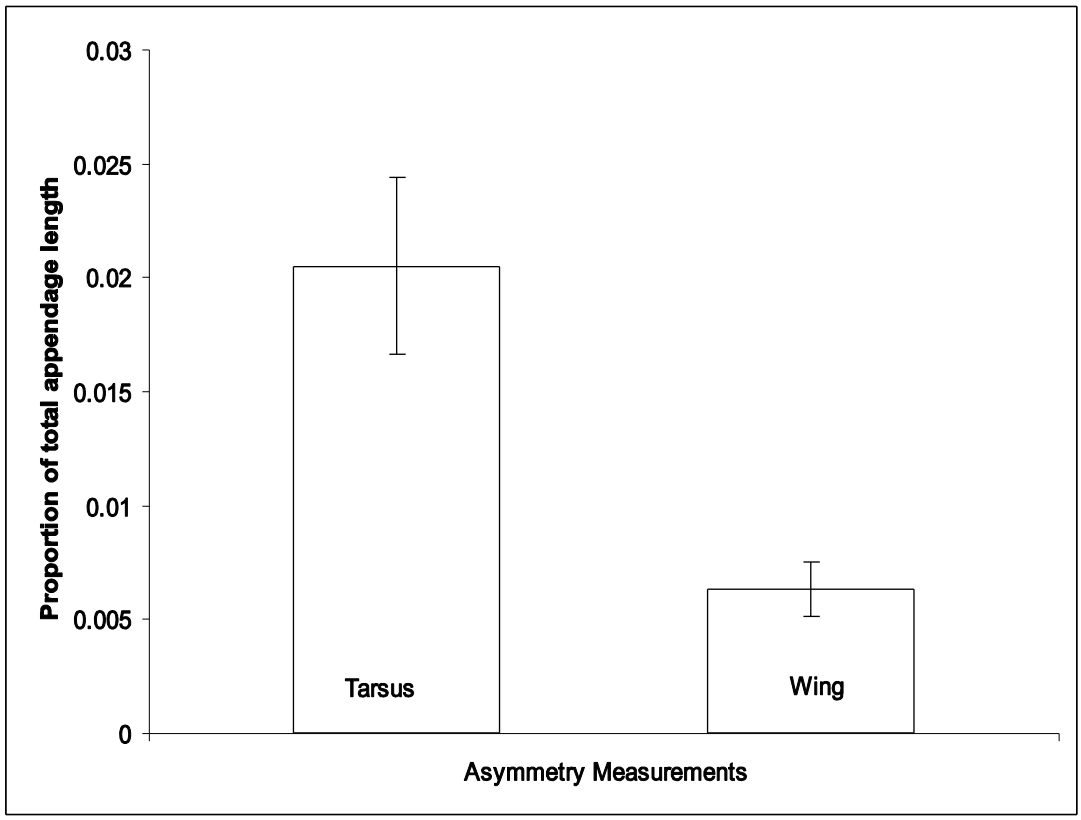

Figure 1.2. Bar graph showing the means and standard error of asymmetry proportions for both wing and tarsus measurements. The tarsi were significantly more asymmetrical than the wings (t-test, two-tailed, p<0.001).

Discussion

The results of our experiments suggest that tree swallows do not express functional asymmetries or laterality during obstacle-avoidance in escape-flight and suggest constraints imposed by selection for morphological symmetry are responsible. Tree swallows chose the larger opening in trials 2 and 3 of both experiments; because tunnel experiments involve collisions with the sides of the tunnel when flying through small openings (DJC and DWW, unpublished data), we define the larger opening as the less risky, and optimal, choice. However, as evidenced by the results of trial four in experiment one, the smaller opening was not so small as to prevent birds from flying through it. Tree swallows failed to respond in a consistently lateral manner to symmetrical obstacles in trials 2 and 4, suggesting that these birds do not express functional asymmetry during in-flight escape behaviours at a level of strength detectable by this study.

However, it is possible that with increased overall sample size and a revised experimental protocol that increases trials by individual birds, more subtle expressions of side bias could be found. An exploration of other in-flight behaviours such as predator avoidance, hunting, and conspecific approach could also yield an expression of side bias not seen here in our obstacle-avoidance trial. A third possibility is that swallows approach and evade obstacles in a way that avoids the negative consequences of side bias. Moreover, an individual's behaviour during flight might be a combination of expressed side bias and flight movements that counteract side bias.

Although there are strong links in birds and mammals between brain lateralization and behavioural lateralization (in pigeons, Prior *et al.*, 2002; Prior *et al.*, 2004; in chicks, Deng and Rogers, 1997), functional wing symmetry is

critical for anatomical, biomechanical, and energetic features of flight (Norberg, 1990; Hambly *et al.*, 2004). In tree swallows, both side-bias (Peterson, *et al.*, 2001) and morphological asymmetry in tarsus, bill, and primary feather lengths (Teather, 1996) has been reported. However, repetitious behavioural side-bias can cause morphological asymmetry (Adam, *et al.*, 1998) and conservation of wing symmetry is likely at odds with the expression of laterality and behavioural side-biases in flight. This is supported by comparison of our anatomical and behavioural results, first, asymmetries in individual tarsus lengths varied an order of magnitude more than did those found for individual wing lengths (Figure 1.2), and, second, these relatively small intra-individual differences in wing length did not predict either initial side choice or side preference in the tunnel (Figure 1.1).

Ground and aerial hawking foraging strategies are likely subject to different regimes of selective forces. Within flight, different behaviours might also warrant differing expressions of side-bias; predator avoidance, in which the risks are much higher, or conspecific approaches, in which detailed perceptual evaluation is necessary, might carry an expression of side bias. Over evolutionary time, we expect trade-offs between flight performance and hemispheric specialization; for substrate-based activities, we expect, similar trade-offs should be less extreme. Our results suggest that hemispheric specialization, as expressed through side-biases, may not be tightly correlated under all sensoribehavioral conditions. In birds, chicks (Dharmaretnam and Rogers, 2005; Vallortigara *et al.*, 1996; Deng and Rogers, 1997), pigeons (Deng and Rogers, 1997; Prior *et al.*, 2002; Prior *et al.*, 2004), Australian magpies (Rogers and Kaplan, 2006) and stilts (Ventolini *et al.*, 2005) all show behavioural lateralization in at least some substrate-borne activities (e.g.,

copulation, substrate-borne foraging). Pigeons have clear structural and functional asymmetry of the brain and show behavioural lateralization (Gunturkun and Kesch, 1987; Buschmann *et al.*, 2006). Additionally, they show functional asymmetries of cue use and homing behaviour while flying (Prior *et al.*, 2004). However, it is expected that, like the swallow, this and other species will not show a strongly lateralized motor response to avoid obstacles in flight due to context dependent costs associated with flying. Studies using guppies (*Poeceliid* spp.) and other fish, in similarly designed escape/avoidance trials, report both functional asymmetries and laterality (Bisazza *et al.*, 2000). Side preference varied with the type of obstacle, maintenance of visual contact with the goal, and phylogeny. We suggest that the difference between these results from swimming fish and those from our study using flying tree swallows supports our contention that competing constraints unique to behavioural context and to powered flight leads to the lack of functional asymmetry in obstacle avoidance trials.

Degree of lateralization and coordination of functional asymmetry at the population-level both vary with gregariousness in fishes (Bisazza *et al.*, 2000). Tree swallows fly in large flocks and roost communally when not breeding (Winkler, 2006); however, in contrast to European starlings, *Sturnus vulgaris* and other birds, flocks do not exhibit any group level polarity of direction (Robertson *et al.*, 1992). In order to separate the existence of laterality from its expression in flying birds, as well as the strength and context of an effect, further research is required. Limiting visual pathways (Gunturkun and Kesch, 1987; Prior *et al.*, 2004) during a flying obstacle avoidance trial might lead to the expression of a masked trait. In addition, varying the scope of the trial or the placement and type of visual cues (Bissazza *et al.*, 1997) could further

define the contexts under which laterality will be expressed or masked. Additionally, future research could try to tightly couple equivalent substrate-born decisions with an in flight decisions of side bias; establishing such comparable experiments in quite different contexts would be challenging but worthwhile.

Research into laterality often uses side-bias as a means of detecting hemispheric specialization (Ventolini *et al.*, 2005). However, in situations where expression of laterality is disadvantageous, masking could occur. We suggest that a potentially rewarding avenue for future research consider information acquisition and decision-making in light of potential trade-offs between the behavioural and morphological outcomes of these processes and pervasive vertebrate hemispheric specialization and expressed or masked side-biases under a broad range of ecological contexts and contingencies.

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CHAPTER 2

TURKEY VULTURES USE ANTHROPOGENIC THERMALS TO EXTEND THEIR DAILY ACTIVITY PERIOD

Mandel JT, Bildstein KL (2007). *Wilson Journal of Ornithology*. 119:102-105.

Abstract

We describe predictable nocturnal soaring flight in Turkey Vultures (*Cathartes aura*) feeding at a landfill in eastern Pennsylvania. Birds feeding at the landfill returned to their roosts each evening by gaining altitude while soaring in thermals above flared methane vents at the site. Our results highlight behavioral plasticity in this species, which, in part, may explain why Turkey Vultures are so common throughout much of their extensive range.

Introduction

Turkey Vultures (*Cathartes aura*) are energy minimizers like most avian scavengers (*sensu* Schoener, 1971; Ruxton and Houston, 2002). Individuals at rest maintain low metabolic rates for their body mass and reduce their core body temperature at night in apparent efforts to conserve energy (Heath, 1962; Wasser,1986). Turkey Vultures in flight usually soar and glide when flying between roosts and previously located food, when searching for new sources of food, and during migration (Pennycuick, 1972; Mundy *et al.,* 1992; Kirk and Mossman, 1998; Ferland-Raymond *et al.,* 2005). At times, the species engages in intermittent flapping flight, particularly when departing from and descending into their roosts. This behavior is generally rare except when updrafts are unpredictable or weak. Our observations, assisted by radio tracking, indicate that lack of sufficient assisted lift can ground individuals

several days or more (J. Mandel, pers. observ.). Turkey Vultures have long been known as “late risers” (Ludlow Griscom in Bent, 1937) that usually restrict their daily activities to mid morning to late afternoon when thermal- and slope-soaring are possible (Kirk and Mossman, 1998).

Anecdotal and possibly disturbance-induced nocturnal flight has been reported in the species (Tabor and McAllister, 1988) but regular nocturnal flight is unknown. Here, we report regular nocturnal flight in Turkey Vultures returning to their roosts in the evening after soaring in anthropogenic thermals created by flared methane at a landfill in eastern Pennsylvania.

Methods

We watched Turkey Vultures on 120 non-rainy days from 12 July to 5 November 2004, and from 20 June to 17 July 2005, at a 45-ha Waste Management, Inc. landfill in Pen Argyl, Northampton County, Pennsylvania (40° 52’ N, 75° 15’ W). Birds were observed continually from 0730 to 2315 hrs EST, with a three-hour break from 1300 to 1600 hrs EST. Observations were from an unused hilltop on landfill property, with the farthest roost being ~300 m. Adequate artificial lighting at the site permitted nocturnal observation without special equipment. Prior to the observations detailed here, we observed vultures at three communal roosts near the landfill for 20 days in June 2004 and for 47 days in July and August 2003. Our roost-site observations, which were conducted from dawn until dusk, and included both unmarked individuals and radio-marked birds, are used here to establish a temporal baseline for vulture behavior in the area.

Methane is vented at two sites at the landfill. One site, the “big flare,” consists of a group of three 10-m-high vent pipes. The other site, the “little

flare," consists of a single 10-m vent pipe. At both sites methane is flared continuously, around-the-clock, 365 days a year.

Observations

Between 30 and 90 Turkey Vultures fed at the landfill daily. On more than 70% of the days, 10 to15 individuals fed until 2100 to 2300 hrs EST, or approximately 90 to 210 min after local sunset. We do not know whether the late-feeding birds were the same individuals each day, or whether a larger subset of the population engaged in late feeding on an occasional basis. Vultures that fed in farmlands, woodlands, and suburban areas near the landfill returned to their roosts before 2000 EST or, at most, 30 min after the local sunset.

Turkey Vultures that left the landfill used both natural thermals and anthropogenic thermals at the methane vents throughout the day to gain lift before departing the site. When natural thermals were no longer available after sunset, vultures that left the landfill initially approached the vents in flapping flight, and then circle-soared to approximately 100-200 m in thermals above the vents before gliding in the direction of nearby roosts. On most days, 10 to 30 vultures arrived at the landfill before 0800 hrs EST, soared above the vents for several minutes, and then departed, presumably for more distant feeding sites.

Turkey Vultures feeding at the site roosted in three communal roosts within 4 km of the landfill. Two of the roosts contained 30-50 Turkey Vultures and 5-10 Black Vultures (*Coragyps atratus*). A third roost contained 10-15 Turkey Vultures. Black Vultures at times fed at the landfill but none remained as late in the day as Turkey Vultures, and none soared in thermals above the vents.

Discussion

Thermals created by flared methane appeared to be considerably stronger and hotter than nearby “natural” thermals. Vultures soaring above the vents ascended more rapidly than those soaring in nearby natural thermals, and many appeared to have difficulty maintaining level flight while doing so. Most of the birds that flew within vent thermals did so intermittently, and rather than circle-soaring radially about the center of the thermal while ascending constantly, circle-soared tangentially within the thermal for brief periods and then circle-glided outside the thermal for longer periods (Figure 2.1). We believe that individuals did so because they were not able to soar continually within the vents. Workers at the site reported finding Turkey Vulture carcasses at and near the bases of the vents, suggesting that in addition to providing soaring opportunities for vultures, the anthropogenic thermals at the vents also killed them, most likely either by scorching or suffocating individuals. Thus, the vents may have created an “ecological trap” for the birds that used them (Schlaepfer, 2002).

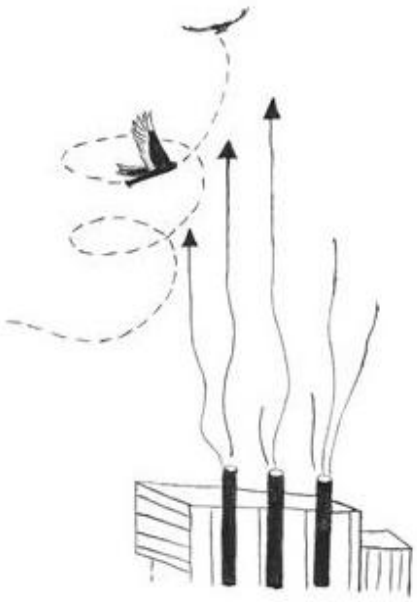

Figure 2.1. The “big flare,” the main methane vent facility at the Waste Management, Inc., landfill in Pen Argyl, Pennsylvania. Vultures soaring with the thermal created by the flared methane at the vents do so tangentially, rather than radially.

That Turkey Vultures, but not Black Vultures, soar in vent thermals at this site may be due several factors. First, many vultures that roosted nearby searched for carrion in the surrounding landscape rather than for food refuse at the landfill, suggesting that food was limited at the landfill. We tested this hypothesis by placing a road-killed deer (Odocoileus virginianus), a road-killed raccoon (Procyon lotor), and a butchered chicken (Gallus domesticus) at visible locations at the site to examine the extent of competition for food. Up to six Black and Turkey vultures fed upon the chicken simultaneously, and up to 14 individuals fed simultaneously upon the deer. Black Vultures dominated Turkey Vultures at feeding sites, suggesting the former may be able consume sufficient food without prolonging the length of their feeding day. Second, Turkey Vultures typically hold their wings in a pronounced dihedral when flying

low over the landscape, a self-righting aerodynamic “design” that stabilizes their flight in turbulent air (Mueller 1972), whereas as Black Vultures do not. The relatively turbulent nature of thermals above the vents may have precluded their use by Black Vultures.

That Turkey Vultures are able to lengthen their daily activity periods via use of anthropogenic thermals suggests considerable behavioral flexibility in the species. This may help explain its large range and relative abundance.

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CHAPTER 3

THE MOVEMENT ECOLOGY OF MIGRATION IN TURKEY VULTURES

Mandel JT, Bildstein KL, Bohrer G, Winkler DW (2008). *PNAS*. 105: 19102-19107

Abstract

We develop individual-based Movement Ecology Models (MEM) to explore Turkey Vulture (*Cathartes aura*) migration decisions at both hourly and daily scales. Vulture movements in 10 migration events were recorded with satellite-reporting GPS sensors, and flight behavior was observed visually, aided by on-the-ground VHF radio-tracking. We used the North American Regional Reanalysis dataset to obtain values for wind speed, turbulent kinetic energy (TKE), and cloud height, and employed a digital elevation model for a measure of terrain ruggedness. A Turkey Vulture fitted with a heart-rate logger during 124 hours of flight during 38 contiguous days showed only a small increase in mean heart rate as distance traveled per day increased, confirming that soaring flight is passive and that flight mode does not become progressively more active with distance. Data from 10 migrations for 724 hourly segments and 152 daily segments showed that vultures depended heavily upon high levels of TKE in the atmospheric boundary layer to increase flight distances and maintain preferred bearings at both hourly and daily scales. We suggest how the MEM can be extended to other spatial and temporal scales of avian migration. Our success in relating model-derived atmospheric variables to migration indicates the potential of using regional reanalysis data, as here, and potentially other regional, higher resolution, atmospheric models in predicting

changing movement patterns of soaring birds under various scenarios of climate and land use change.

Introduction

Traditionally, bird migration has been treated separately relative to other movements within an individual's life history (Bildstein, 2006; Newton, 2008). Although long-distance migration operates on different scales and produces different patterns than those of other movement types in a bird's life cycle, there are also many similarities (cf. Dingle, 1996). As in other biotic movements, migration involves the assessment of internal state of the organism, external factors, and past behavior in order to make decisions about motion and navigation (Nathan *et al.*, 2008).

One significant challenge of migration research is measuring the extent to which migratory routes and schedules of individual migrants are influenced by external factors, including wind direction and speed (Thorup *et al.*, 2003; Thorup *et al.*, 2006), food availability and habitat (Newton, 2008), and the behavior of other migrants (Bildstein, 2006; Pennycuick, 1998). One important axis of variation among migratory birds is the extent to which environmental factors act as facilitators of, as opposed to barriers to, movement. Determining the effects of environmental factors is particularly important for soaring birds, whose movements rely upon environmental factors such as deflection updrafts and thermal convection as their principle means of propulsion. Whereas those using primarily flapping flight are, in principle, not directly dependent on environmental forces for lift. Although we recognize that this categorization can be overly simplistic (see, for example, Liechti and Schaller, 1999) and that other categorizations based on ecological function exist (Hedenstrom and

Alerstam, 1995; Alerstam and Hedenstrom, 1998), the dichotomy of soaring versus flapping migration can play a useful role in understanding the internal costs of movement, flexibility of migration timing, and the ability to adopt new routes (Bildstein, 2006; Newton, 2008; and references therein).

Diurnal migrants are an excellent group in which to explore this issue, as they span the full range from soaring migrants (e.g. many raptors, Bildstein, 2006) to flapping fliers (e.g. shorebirds, Piersma *et al.*, 2005). Some migrants, including swallows (Winkler, 2005), raptors (Bildstein, 2006), and bee-eaters (N. Sapir, pers. comm.), switch between flapping and soaring flight modes based on atmospheric conditions. Turkey Vultures are obligate soaring migrants (*sensu* Bildstein, 2006). They rarely travel long distances without the aid of thermals and updrafts, and anthropogenic night-time thermals can increase their daily activity period (Mandel and Bildstein, 2007). Because Turkey Vultures seasonally undertake long-distance movements within an ecological group (i.e., avian scavengers) that traditionally does not, we feel they can be used as a test case, against which future studies of this dichotomy in species that use both strategies can be compared.

Here, we set out a test case to assess the role of external factors and internal state on movement and navigation decisions. We seek to test the hypotheses that a) specific route choices are determined to a large extent by wind, topography, and availability of turbulent uplift. b) The movement ecology framework can be used to formulate a movement equation that describes movement in terms of measurable proximal variables, including environmental variables and lagged distances and bearing deviations, and that this model can be fitted to the data using mixed and linear statistical models and autocorrelation functions; and c) that atmospheric regional-scale-modeling

data can be effectively used to approximate the environmental conditions that affect migration flights. The Movement Ecology framework (Nathan *et al.*, 2008) guides the decomposition of complex movement phenomena into specific behavioral and environmental components. This provides a framework for the combination of meteorological and geographical data and direct observations of migrating birds to elucidate the proximate mechanisms driving vulture migration and to formulate hypotheses about the ultimate (evolutionary) factors driving bird migration.

We focus on estimating the movement decision functions using external factors, internal state, and past behavior by fitting movement and navigation equations; we use weather data from a regional-scale observation-model reanalysis product and digital elevation model to estimate important components of the external factors, and measure heart rate to estimate internal state. Additionally, we evaluate how characteristics of present and preceding movements, such as previous distance, direction, altitude, speed, and autoregressive components of movement, influence subsequent movement.

Defining a Movement Ecology Model (MEM) for migration requires that we "de-compose" migration into different scales of movement: (1) A micro-scale (mm-meters, seconds-minutes), which represents the size of turbulent eddies around the bird and the instantaneous conditions which the bird perceives, and where many decisions about movement take place. Unfortunately, due to the chaotic nature of turbulent flows and the limitations of current computation and measurement ability, it is impossible to know the exact micro-scale conditions that determine a bird's movement. (2) A coarser scale (tens of km and few hours), which provides a convenient source of information, as data

from regional atmospheric models and miniature measurement devices are available at this regional scale. Some tactical decisions about migration movement are probably made at the coarser scale when perceived information is aggregated (e.g. Pennycuick *et al.*, 1979; Shamoun-Baranes *et al.*, 2003; Thorup *et al.*, 2007). For convenience, we refer to this coarser scale as the "hourly scale," and we use the hourly scale as a surrogate to the micro-mechanistic scale to determine how appropriate and useful information at this resolution can be to study migration movement. (3) A daily scale, in which decisions about re-fueling, route choice, and distance to be traveled are set (for example, Hake *et al.*, 2003; Haines *et al.*, 2003; Alerstam *et al.*, 2006). (4) An annual scale, in which birds (or other organisms) assess the success of previous migratory choices and decide on movements accordingly (Fryxell *et al.*, 2008). (5) A life-history scale where broad decisions such as when and where (or if, in the case of facultative migrants) to migrate are set (for example McNamara *et al.*, 1998). (6) And finally, a long-term evolutionary scale in which natural selection on aspects of migration takes place (Berthold *et al.*, 1992). Understanding larger-scale phenomena requires mechanistic understanding at smaller scales. We focus on the hourly and daily scales where empirical data allow direct analysis.

The MEM framework provides an explicit guide to data analysis. Here, we parameterize, at two scales, the MEM controlling the migratory movements of Turkey Vultures. By fitting empirical data to the MEM, we set out explicitly to assess the relative roles of external-factor variables (turbulence, horizontal winds, and topography), internal state (heart rate), and the role of present state (altitude, speed) and past behavior (auto-regressive components of movement) in determining the navigation and movement of a soaring migrant.

Here, we assess navigation at two scales by looking for deviations from a local axis of movement (established based on the previous hours or days of movement); we infer that smaller deviations from a movement axis reflect a more direct route to local goals. Movement is assessed by looking at straight-line flight distances at two scales of movement, hourly and daily. We trapped 12 Turkey Vultures at carcasses in northeastern Pennsylvania and on nests in Saskatchewan, Canada, between August 2003 and November 2006. Of these, seven birds were fitted with GPS satellite tracking tags (Microwave Telemetry, Inc.). A subset of the GPS birds was fitted with inter-peritoneal data loggers that recorded heart rate at 2-second intervals (Biometistics, UK). GPS data on movements were collected at hourly intervals on all birds via the ARGOS satellite network. We were able to record hourly movements in 10 one-way migratory journeys in the seven GPS-fitted birds. These journeys totaled 724 hourly migratory movement segments that met our data quality criteria (described in the Methods below) as well as 152 daily movements. We used close proxies and representative variables to assess the effects of internal state, the role of past behavior, the initial state at each movement leg, and external factors. Mixed-effect linear models were used to fit these data to the MEM at both the hourly and daily scale of migration.

Results

We began with the general MEM (Nathan *et al.*, 2008), and adapted it to address external, internal, and temporal variables in a specific way (see Methods). Essentially, we assumed that a linear combination of the three classes of variables and their interactions would inform a movement decision

function, as well as a navigation-decision function. We then tested these variables statistically.

Ten migration events were successfully recorded in seven birds, including 6 southbound movements in fall and 4 northbound movements in spring. Turkey Vultures caught in Pennsylvania migrated along the east coast of the US, principally to Florida and other areas of the southeast (Figure 3.1). Two vultures caught in Saskatchewan, Canada did not complete migrations, but traveled through the central US before their accidental deaths. All birds were adults ($\geq 3^{rd}$ year). For all seven birds, the longest straight-line distance traveled in a day was 327 km, and the longest straight-line hourly movement was 68 km. Birds did not migrate on 15 of the 152 days (10%). The straight-line distances between successive GPS observations grossly underestimate the total distances traveled, as visually tracked individuals revealed circuitous flight paths.

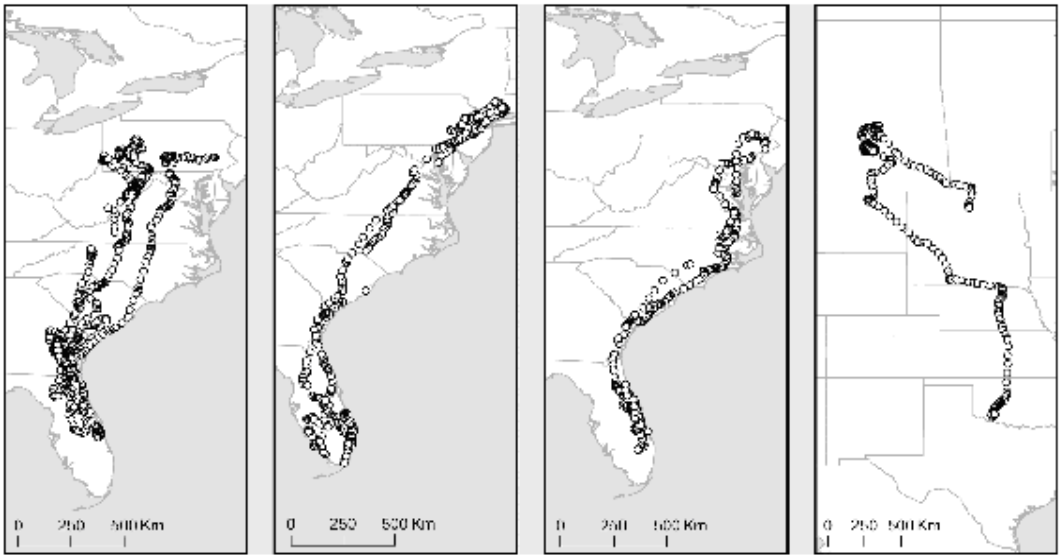

Figure 3.1. A map of the migratory movements. The final panel shows the two migratory tracks that originated in Saskatchewan, while the first three panels show the migrations of Turkey Vultures that were captured in Pennsylvania.

We measured field heart rate successfully in 1 bird during 38 days of southbound migration. An analysis of the heart rate (Figure 3.2) showed it to be determined in only small part by distance; this suggests that, unlike flapping, soaring flight does not lead to greatly increasing metabolic costs with distance. Much more important in predicting heart rate were the vertical movements of air (as measured by the vertical movement of pressure levels in the model; VVEL), and the ruggedness of the terrain. As mentioned below, rugged terrain can change the spatial structure and consistency of thermals, and this could lead to a less efficient use of atmospheric energy. We hypothesized that movement (both motion and navigation) is an autoregressive process: across scales, distances and turning angles are likely to be dependent on previous movements. We fit the distances and bearing deviations at both the hourly and daily scale to autoregressive integrated moving average models to test the degree and magnitude of any autoregressive components in these time series (Box and Jenkins, 1970). At all scales, movement vectors fit the ARIMA(1,0,0) class of models, which can be interpreted conceptually as a correlated random walk; distances and turning angles were influenced significantly only by the movement immediately preceding. Coefficients of autoregressivity are listed in Table 3.1. Future work, using higher resolution data sources (e.g. Fryxell *et al.*, 2008), may improve the information resulting from autoregressive integrated moving average approaches and bridge the gap between these simple approaches and other movement models such as Lévy walks (Bartumeus and Levin, 2008). In any event, we suggest that appropriate null distributions for the relation to previous states be evaluated as an important part of the analysis of movements.

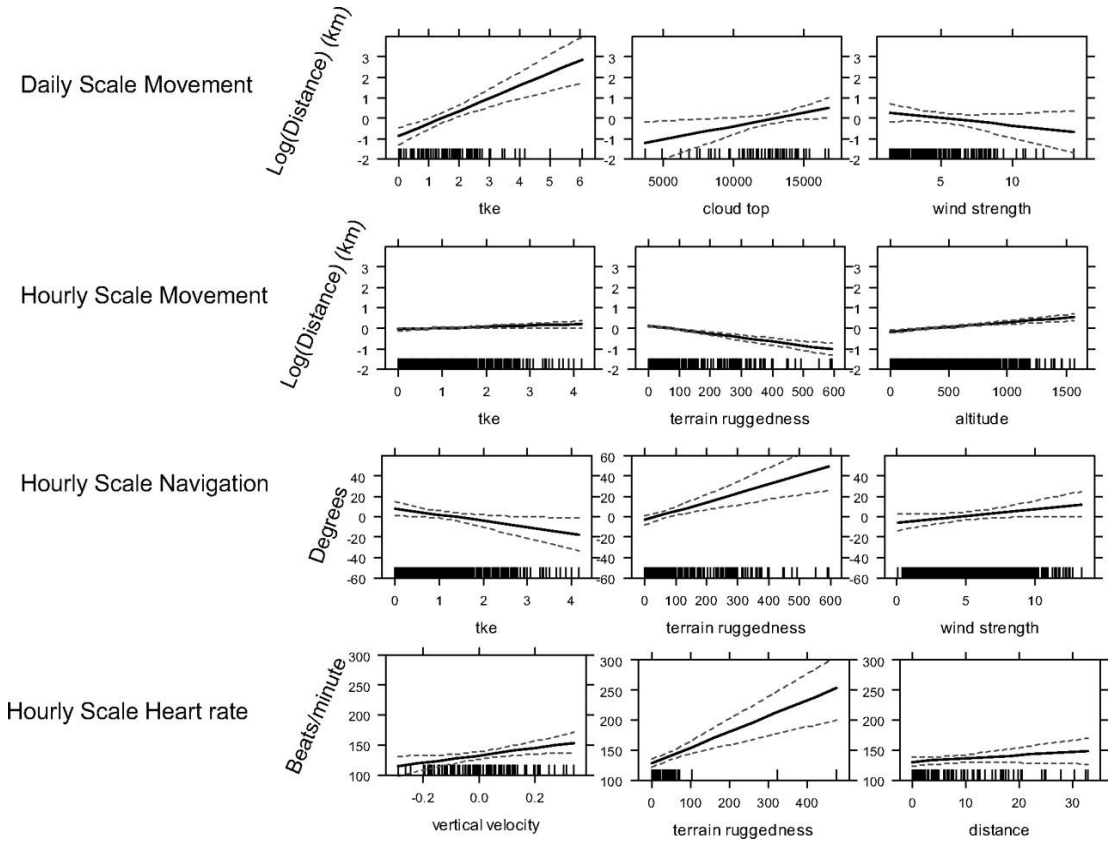

Figure 3.2. Effects plots of the major findings in our statistical analysis. Effects of external factors on daily scale movement, hourly scale movement, hourly scale navigation, and hourly scale heart rate are shown. Plots were generated from the mixed effects linear models summarized in Table 1.

Next, we set out to test the role of external factors (Table 3.1) in determining the distance and turning angles of migration. We used turning angles as an indirect proxy for navigation, and measured this as an angular deviation from an axis of movement established by the previous 7 hours of movement (hourly scale) or week of movement (daily scale). These two scales were chosen to assess the relative roles of scale in studying movement; the hourly scale is the smallest scale that was feasible for us to measure and record standardized data, while the daily scale is a common scale in studies of movement and especially migration. For some birds, we had more than one "migratory event," which we defined as the collection of all daily and hourly

movements in a given (fall or spring) migration season. Mixed effect models were run with random effects for individual movement events nested within migratory events, which were in turn nested within birds. There were no significant random effects for birds or migratory events at the scales we examined (p>0.5).

Table 3.1. Summary of observed effects. Variables are divided into three categorical groups: external factors (*r*); temporal factors (u_t); and their interaction ($r \times u_t$). Motion is measured using distance as a dependent variable, and navigation is measured using angular deviation from a local mean. The influence of past positions was assessed through auto-regressive integrated moving average modeling for the correlation structure. All other variables were independent main effects. Angle models used degrees, and negative coefficients indicate less deviation and thus a straighter path. All two way interactions within and between the external effects and temporal variables were tested. The only significant interaction was between Terrain Ruggedness and TKE. Information is organized as follows: parameter estimate (standard error) significance, where NS : not significant; ± : p<0.1; * : p<0.05; ** : p<0.01; *** : p<0.001.

Group	Cate-gory	Variable	Motion		Navigation	
			H	D	H	D
R	Geo-graphy	Terrain Ruggedness	-0.0006 (0.00036) ±	NS	0.070 (0.024) **	0
		Latitude	NS	NS	-2.7 (0.596) ***	NS
	Meteo-rology	Turbulence kinetic energy	0.085 (.034) **	0.640 (0.11) ***	-6.48 (2.49) ***	NS
		Vertical wind velocity	NS	NS	NS	NS
		Horizontal wind speed	NS	-0.12 (0.047) **	1.43 (0.81) ±	NS

Figure 3.1 (Continued)

		Horizontal wind direction	NS	NS	NS	NS
		Cloud top height	NS	0.0001 (0.00005) **	NS	NS
	Food availability	Inferred by EM approach	NS	-4.3 (0.81) ***	NS	3.01 0.52 ***
T	Motion Navigation Effects	Distance (Motion)			-0.657 (0.179) ***	0.13 (0.055) **
		Bearing deviation (Navigation)	-0.0018 (0.00044) ***	0.234 (0.089) **		
	Past behavior	Altitude at start	0.00036 (0.00009) ***	NS	NS	NS
		Speed at start	0.0068 (0.001) ***	NS	NS	NS
	Autoregressivity	Past position – AR(1) correlation coefficient		0.48	0.33	0.32
R:T	Interactions	Terrain Ruggedness:TKE	-0.00068 (0.00022) **	NS	NS	NS

Bearing deviations, our proxy for navigation decisions, were included as a variable in movement models, and movement (log distance) was included as a variable in navigation models. Bearing deviation had a negative association with distance traveled at an hourly scale and a positive association at the daily scale. This suggests that, hour-to-hour, birds are less likely to travel far if they

are off-course. And at the daily scale, this result is likely due to the smaller distances and larger number of days traveled in a southeastern direction during the predominantly fall migratory events analyzed (Figure 3.1).

Distance traveled was most strongly affected at both hourly and daily scales by turbulent kinetic energy (TKE), higher values of which were correlated with increased distance traveled (Figure 3.2). Air movements represented as TKE result either from thermal convection or the shear of horizontal winds by the surface. In most situations, TKE generated by thermal convection results in larger, more structured air movements that are often used by soaring birds (cf. Berthold, 2001); however, birds that migrate along mountain ridges are likely taking advantage of shear-generated TKE. At the daily scale, cloud-top height, which indicates the strength of convective activity in the atmospheric boundary layer, had a strong positive effect on distance traveled. The role of this larger-scale atmospheric indicator is visible only at a larger scale of analysis, reinforcing the importance of scale in defining the scope of inference in studies such as this.

Terrain ruggedness had a negative effect on distance traveled, though this main effect was not as strong in magnitude as the positive effect of TKE. Terrain ruggedness had a very strong interaction, however, with TKE: ruggedness had large negative effects on distance traveled only at high values of TKE, suggesting that, on days with strong convective air-flow, ruggedness can act to decrease the spatiotemporal predictability of uplift and to decrease the coherent length scale of the spatial structure of thermal convection over rough terrain (e.g. Stewart *et al.*, 2002). The birds in this study primarily migrated along level ground where ruggedness is likely to disrupt otherwise predictable thermals, but other raptors that migrate along the Appalachian

chain of mountains clearly benefit from the organizing effect of mountain ridges on wind-generated TKE (Wiemerskirch *et al.*, 2000) .

Wind speed had a negative effect on distance traveled at the daily scale. The negative effects of terrain ruggedness and horizontal winds together with the positive effect of TKE suggests that it is the thermal-convective component of TKE that most enables soaring and migratory movements in Turkey Vultures. As with distance, TKE had a strong effect on navigation (bearing deviation); high values of TKE strongly reduced the bearing deviation. This suggests that whenever uplift in the form of convectively generated TKE (i.e., thermals) is readily available, birds are able to fly in their preferred direction, whereas when there is less available uplift, deviations from the preferred direction of travel in search of useful energy are required to maintain passive flight. Strong winds increased bearing deviations; and cross winds are likely to cause wind-drift and blow the birds off their intended course, as in other raptors (Bildstein, 2006; Berthold, 2001). Terrain ruggedness also increased bearing deviations; a rugged landscape can disrupt the structure of convective cells, decreasing the availability of atmospheric energy in the preferred direction. Such landscapes interact with cross-winds to generate uplift along valley edges and topographic peaks, which may tempt vultures off their principal axis of movement.

At the hourly scale, but not at the daily scale, flight altitude and speed measured at the start of the movement vector had positive effects on the distance traveled: birds that started a vector flying high and fast had more momentum and potential energy to travel farther. Thus, birds at this scale are more likely to fly long distances when they are headed in the preferred

direction (i.e., the regional principal axis of migration). Full statistical models for all these results are presented in Table 3.1.

Discussion

Migrants move and navigate in response to a host of external, internal, and temporal factors. Using a range of meteorological, geographical, and internal variables, we found support for the hypothesis that proximate route choices are affected by external meteorological and topographic factors. Increasing flight distances had a relatively small effect on measured heart rate. External factors, such as rugged terrain and the vertical movements of pressure levels in the atmosphere had a relatively large effect on observed heart rate during migration (Figure 3.2). Given the relatively small magnitude of variations in heart rate during flight, a detailed look at the effects of external factors on movements is appropriate.

In any study of movement, a detailed look at scales of movements and scopes of inference is critical. We have focused on two scales: an hourly scale and a daily scale. The hourly scale represents the semi-stationary meteorological conditions, including wind and turbulence statistics, and it is the finest scale where meteorological data are available over large domains. In this study it acts as a surrogate for the micro-mechanistic scale, whereas the daily scale is common in migration studies. Scale restrictions can have implicit drawbacks: the hourly scale, for example, grossly underestimates actual movement, and thus becomes less appropriate for assessing tortuosity in studies of orientation.

Turkey Vultures appear to depend on convectively generated TKE to supply the necessary vertical movement of air for their movements. The

species exerts little additional energy during flight, and, as in albatrosses (Weimerskirch *et al.*, 2000), long-distance movements do not strain the birds energetically more than do short-distance flights.

Several previous studies have looked at the relationship of soaring birds to convective and sheer turbulence using direct observation and found that use of thermals for soaring varies with species, body size, behavior, time of day and thermal intensity (Pennycuick *et al.*, 1998, Shamoun-Baranes *et al.*, 2003; Bradbury, 2000; Spaar and Bruderer, 2000; Shannon *et al.*, 2002). The Turkey Vulture's ability to soar effectively in turbulent winds may be enhanced by its dihedral wing profile, which is inherently more stable than that of birds that soar with a horizontal wing profile (Mueller, 1972) and may be particularly important in situations in turbulent conditions within the atmospheric boundary layer but close to the ground (Geiger, 1961). Our findings of the role of horizontal winds contrast with those of Thorup *et al.* (2003) on the effects of wind on migrating Ospreys (*Pandion haliaetus*) and Honey Buzzards (*Pernis apivorus*), which do not have a dihedral wing shape. These birds, adapted for more direct flight, engage in wind-drift compensation (Thorup *et al.*, 2003). We did not detect wind-drift compensation in the Turkey Vultures we followed. Rather, they showed increased deviation from the regional principal axis of migration (i.e., uncompensated wind drift) and traveled shorter distances in high winds irrespective of their direction. One likely explanation for this is that wind-drift compensation in vultures happens at a scale different from the scales explored here. Indeed, it is not likely that our analysis would detect responses to wind that happen at the micro-mechanistic scale, or at fairly large, strategic scales in the migration.

Our results show that TKE data generated by an open, regional-scale, meteorological dataset derived from the simulation results of a regional model, can serve as a surrogate measure for the intensity of thermals. This suggests a new avenue for studying use of turbulence in flying birds. The NARR meteorological dataset is a regional model product, informed by a large number of observations. Unlike direct meteorological observations, NARR is available over large domains in space and time. Even though the spatial and temporal resolution of the NARR model is much coarser than the physical size and turn-over time of eddies that generate TKE, the model parameterization appears to be sensitive enough, and the bird response strong enough, to show a significant correlation between the two. This indicates that data at a regional resolution of a few km^2 and a few hours can be used as a substitute for high-resolution micro-mechanistic scale turbulence data, which to date has been impossible to obtain along a large portion of a migratory path. Customized runs of higher resolution regional atmospheric models and large eddy simulations, which resolve turbulent motion in the ABL (e.g., Backman and Alerstam, 2003), together with more detailed physiological techniques, may also help confirm and extend these findings. This is important, as a major shortcoming of this study is that several of our major results are based on surrogates, including heart rate for energy expenditure, TKE for thermal convection, and terrain ruggedness for a “thermal-dissipating force”. Atmospheric models, which are a major tool in studying and predicting the effects of regional and global climate changes, the ecological effects of land-use changes (e.g., Bohrer *et al.*, 2008; Jackson *et al.*, 2005; Wright *et al.*, 2008), and bird flight (Thorup, 2003; Shamoun-Baranes *et al.*, 2003; Shamoun-Baranes *et al.*, 2006; Nathan *et al.*, 2005) could be used to build on

these equations of movement to test specific ecological and conservation-related hypotheses. By understanding movement-decision functions in the context of this class of models, we will come much closer to being able to predict future migration patterns as well as details of soaring flight under different future scenarios.

Our work with vultures suggests a way to understand the migration decisions that are being made and the integration of external factors that drives these decisions. This work also shows that the MEM can be approached empirically and that data can inform the relative strengths of linkages among factors and state variables. We think this MEM work can serve as the foundation for increased understanding of movements by focusing further empirical work on especially interesting systems and by serving as a basis for more strategic (i.e. adaptive) models of bird migration.

Methods

Assembly of database: We assembled hourly-movement vectors coded in radial coordinates from the GPS movement data. Radial coordinates have the advantage of (a) uncoupling the strong correlation of movements in the X and Y direction in both movement and wind speed, (b) properly weighting large changes in direction on small movement days, and (c) conceptually separating the ability to fly long distances with the direction of flight. In radial coordinates, it becomes necessary to establish a principal axis of movement, and to measure angles (of both wind direction and movement) in terms of deviations from that axis of migration. In addition, the interaction of wind speed and direction becomes a critical measure for interpreting the appropriate effects of wind.

Because the migratory journeys examined consisted of multiple legs with different dominant bearings, we rejected the idea that we could choose a single axis of migration for all points along the migratory journey. Instead, for every movement vector, we used the bearings of the previous seven movement vectors to establish a direction of movement; we term this the local axis of migration. We then took the absolute value of bearing of the movement vector minus the local axis of migration; we termed this the bearing deviation. Wind directions were calculated in the same way, as a bearing minus the local axis of migration; we termed this the wind deviation. Thus, a wind deviation of zero would be considered a tailwind, whereas a wind deviation of 90 degrees would be a considered a crosswind. Following Oliveira *et al.* (1998), we used bearing and wind deviations that were less than 90 degrees to fit linear models. All angle calculations were done using the "Circular" package in R v. 2.3.1 (Ihaka and Gentleman, 1996; Lund and Agostinelli, 2007), which uses a wrapped Cauchy distribution as the null distribution.

After discarding data from non-migratory birds (i.e., birds that didn't show seasonal latitudinal shifts greater than summer latitudinal variance) and poorly performing transmitters, our dataset consisted of 10 migratory events from seven birds. To calculate latitudinal variance, we measured the maximum and minimum latitude in June and July. If birds did not exceed the minimum summer latitude and cover a latitudinal range greater than there summer range during the fall (October and November), we considered them non-migratory. We adopted a conservative filter for hourly scale analysis that consisted of a movement of at least 4 km, during the months of October, November, April, and May, and during which both the beginning and end of each hour was successfully recorded by the GPS loggers (i.e. there are

consecutive hourly measurements on the GPS that can bound an hour of movement). Months for filtering were selected by examining the timing of the beginnings and ends of migratory tracks visually within our data, and determining the months of peak migration from counts at migration watchsites (Zalles and Bildstein, 2000). The distance minimum was calculated by iteratively plotting the density function of mean bearing of movement using an increasing distance minimum. The break-point at which a normal distribution of bearings with a stable standard error emerged from the initially uniform distribution of bearings was found to be the 4-km distance minimum. For daily scale analysis, days were calculated as 0600 hours to the following 0600 hours in the local time zone. Points where the bird was within the above migratory months and between the beginning and end of latitudinal movements were included, except for those in which the beginning and end of the 24-hour period were not both measured successfully. A total of 154 daily movements fit these criteria.

We first examined spring and fall movements examined separately. Finding no difference between fall and spring movements (graphed distributions were visually indistinguishable, and t-tests of logged distances, bearings shifted 180 degrees, and total durations between spring and fall were all >.5), spring bearings were shifted 180 degrees and merged with fall movements. The month of data collection was retained as a main effect. Distance was log-transformed to satisfy assumptions of normality.

Equations of Motion: We derived 2 equations from the MEM, using equations 2 and 3 of Nathan *et al.* (2008), respectively, to describe the motion, Ω, and navigation, Φ, decision functions for Turkey Vultures. These structured our analyses. We used the straight line (i.e. loxodrome route)

distances at two scales as a proxy for motion, and bearing deviations as a proxy for navigation. We generated a series of independent variables that represented internal state, *w*, external factors, *r*, and temporal qualities, u_t, that might influence the bird's MEM decision. We used a statistical model to identify the relevant dependent variables at each scale and estimate their coefficients in a generalized equation structure, which represent a linear combination of all external, internal, and temporal terms, as well as interactions and auto-correlations, affecting the movement and navigation of a passive migrant:

$$\Omega = \sum_k J_k^{r,m} r_k + J^{w,m} w + \sum_k J_k^{u_t,m} u_{tk} + \sum_{k1}\sum_{k2} J_{k1,k2}^{r\times r,m} r_{k1} \times r_{k2} + \sum_{k1}\sum_{k2} J_{k1,k2}^{r\times u_t,m} r_{k1} \times u_{tk2} + J^{\Phi}\Phi + \sum_a J_a^{\Omega}\Omega_{t-a}$$

$$\Phi = \sum_k J_k^{r,n} r_k + J^{w,n} w + \sum_k J_k^{u_t,n} u_{tk} + \sum_{k1}\sum_{k2} J_{k1,k2}^{r\times r,n} r_{k1} \times r_{k2} + \sum_{k1}\sum_{k2} J_{k1,k2}^{r\times u_t,n} r_{k1} \times u_{tk2} + J^{\Omega}\Omega + \sum_a J_a^{\Phi}\Phi_{t-a}$$

Where subscripts *k, k1, k2* are indexes over all the variables in a categorical group. A subscript *a* is an index for time-lag (in integer units of hour or day). Interaction terms are marked with an $\times$. *J* is the model coefficients for the variables, which we estimate statistically. A superscript for *J* marks the categorical group and the MEM variable (m,n for motion and navigation, respectively) it is associated with, and a subscript is a counter. We fit an autoregressive correlation structure to the dependent variable, which is represented by the final term in the equations; this accounts for the fact that all movement decisions must be viewed through the lens of previous movement. Because the vultures we tracked are strictly passive migrants, these equations represent the components within a single motion mode. They do not include the more complex model structure and decision parameters for switching between motion modes. While all of the following variables were considered, only the variables that had significant contributions were included in the final model.

Predictive Variables: We calculated predictive variables in the following three categories: External; Internal; and Temporal.

External variables: Meteorology – Meteorological variable values were taken from the National Center for Environmental Prediction (NCEP) North American Regional Reanalysis (NARR) dataset. NARR (Mesinger *et al.*, 2006) is a product of the ETA regional model (Janjic, 1994) forced with a large set of satellite, surface and balloon observations. It consists of a 3-dimensional grid that covers all of North America with a horizontal resolution of 32x32 km^2, a vertical resolution defined along pressure levels, and a temporal resolution of 2 minutes. Snapshot and time averaged data are saved every 3 hours.

The bird's longitude and latitude were matched with the nearest NARR grid-cell center. NARR data for that cell were interpolated linearly in time to the timestamp of the bird GPS data point. For 3-dimensional variables, we interpolated vertically between the NARR variable values for pressure levels height (HGT) closest to the GPS-determined altitude of the bird. Four meteorological variables were included: (1) Wind speed and wind direction, processed from the NARR variables for latitudinal and longitudinal wind velocities (UGRD, VGRD, respectively). Horizontal winds were translated into polar coordinates, the angle was translated into a deviation from a local mean direction of movement; (2) TKE, which is parameterized in NARR using empirical relationships between surface fluxes and the stability of the atmospheric boundary layer (ABL) (Mellor and Yamada, 1982). High TKE is typical for days with intermediate wind levels and strong convective heat flux from the ground (cloudless hot days), and is indicative of large thermals; conversely, days with very strong winds, neutral boundary layer conditions and strong mechanical shear can also produce high values of TKE (referred to

here as “shear” TKE; Stull, 1988). (3) Pressure vertical velocity (VVEL) is defined as the rate of change over time of the height of the pressure levels, which make up the vertical dimension of the grid. The vertical movement of pressure surfaces is associated with the daily cycle of ABL dynamics and mesoscale pressure fronts. (4) Cloud-top height, a two-dimensional model field, indicates the strength of parameterized convective activity in the ABL. To eliminate strongly cross-correlated variables (such as cloud base, cloud depth, and cloud top) from the model, we ran each variable separately in a mixed linear model including all weather components and no interactions, with ln(Distance) as the dependent variable. Cloud top height was found to be the variable with the best fit using AIC, BIC, and log-likelihood, and therefore, was included in the final model and the other two, cloud base, and cloud depth, were discarded.

Geography. – We used the GTOPO30 digital elevation model (DEM) available from the EROS database at the USGS, which has grid spacing of 30 arc seconds (~1 km). We created a map of terrain ruggedness based on the variance in altitude of adjacent grid cells using Manifold v. 2.1. Terrain Ruggedness was calculated according to the formula provided by Riley *et al.* (1999), and provides a unitless index of variance in elevation.

Internal variables

Energetics. – We modeled the role of internal state in migratory Turkey Vultures using heart rate as a representation of the cost of movement. Six heart-rate loggers were deployed; 3 were recovered. One heart-rate logger worked successfully for a period of 38 days, during which the vulture carrying it flew from northern Pennsylvania to southern North Carolina. This bird’s behavior was monitored visually by Mandel, who followed the bird in a vehicle,

and its positions were monitored by satellite tracked GPS harnessed to the back of the bird. Heart rate was averaged over one-hour periods that correspond to one-hour movement vectors recorded by the GPS. Because of the limited heart rate data, this internal effects model was run separately from external effects using a simple linear model of heart rate *vs*. the log-transformed distance to estimate the cost of movement. Linear models of bearing deviation *vs.* heart rate were run to estimate the physiological cost, if any, of navigation decisions away from the local mean direction of movement. We also ran a linear model with heart rate as the dependent variable, against independent meteorological, geographical, and movement variables, in a similar fashion as the movement models.

Temporal variables - Behavior at the beginning of a movement vector

The speed of travel and flight altitude measured at the start of the movement vector represent the starting state of the migrating vulture at the beginning of any movement vector.

Past behavior estimated auto-regressively – We fit Auto-Regressive Integrated Moving Average (ARIMA) correlation matrices to all the distance and bearing dataset separately to factor in the auto-regressive components of movement. First, we modeled the 10 migratory journeys as random effects in a hierarchical, mixed model (see appendix for full model summaries). autoregressive integrated moving average models were fit to each dependent variable following the methodology outlined by Box and Jenkins (1970), using autocorrelation, partial autocorrelation, and lag plots to assess the degree of auto-regressivity and sampling noise. In all cases, the models consisted of a single autoregressive component. In short, at both temporal scales, movement was modeled as a correlated random walk.

Model Simplification

Statistical analyses of the variables above consisted of mixed linear models created using the "nlme" package in R (Pinheiro *et al.*, 2007). For each mixed model, an *a priori* correlation structure was specified using an autoregressive integrated moving average function. Correlated variables were tested independently against the log-transformed distance, and only the one with the most predictive power was kept. All models began with the inclusion of all main effects and all potentially relevant interactions. Backward selection, on interactions first, using maximum likelihood, was performed to determine the final model. Final models were compared with initial models using ANOVA, and AIC was observed to decrease throughout model selection in all models. Parameter values were estimated using restricted maximum likelihood. The models were compared to identical models without random effects, to determine if the random effects significantly changed the model. This was done by comparing the difference of -2xlog-likelihoods with a chi-square table at 1 degree of freedom.

Statistical Models:

Hourly Distance and Navigation Models

The external effects on motion were modeled using the log-transformed distance as the dependent variable; for navigation, the deviation of bearing from a local mean was used. The variables for external effects and present state are listed in Table 3.1.

Daily Distance and Navigation Models

We created vectors of daily movements for each vulture to determine the role of external effects on migratory movements at an intermediate temporal scale. We averaged wind and habitat variables in scaling our independent

variables from hourly movements to daily movements. For TKE, pressure vertical velocity, and cloud top, which grow throughout the day and have a highly autoregressive daily structure, the maximum for each day was selected. For all variables, distributions of the reduced dataset were compared with the distributions of the original data set to ensure that there was no loss of variability.

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CHAPTER 4

PATTERNS OF WEATHER UTILIZATION BY MIGRATING TURKEY VULTURES IN DIFFERENT LANDSCAPES

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Abstract

Whereas avian migration patterns show enormous diversity in extent, timing, speed, and sociality, determining whether such diversity is a result of different internal strategies or differences in external conditions (e.g. weather) has important implications for understanding migration patterns and forecasting ecological responses to change. Here, we examine migration strategies in response to external conditions in migrating Turkey Vultures (*Cathartes aura*) in North America. We use a customized movement-ecology model (MEM), GPS tracking data, and regional-scale meteorological data to explore differences in movement processes as a function of external state in three populations of turkey vultures which vary in overall migratory distance and in the landscapes they inhabit and migrate through. We find that the terrain a bird flies over has a greater impact on migratory process than the overall distances travelled. Two populations in the East and West coasts of the United States, both of which have access to mountains but differ in migratory distance, had a similar response to weather, indicative of their use of a combination of slope- and thermal-soaring. Continental-interior, “plains populations,” exhibited a different migratory process that is primarily indicative of thermal soaring. These differences have important implications for understanding constraints and motivations of soaring movements, as, unlike

landscape, migratory distance is often used as an identifying characteristic of migration.

Introduction

Traditionally, bird migration has been categorized according to patterns of movement. For example, migratory birds are at times classified as long- or short- distance migrants (Newton, 2008; Dingle, 1996), and at times as obligate or facultative migrants (Winkler, 2005). Although some dichotomous categorical distinctions, such as flapping vs. soaring, are process-oriented and clearly have implications for the physiology, energy budgets, and decision-making processes of birds, others, such as inter- vs. intra-continental, describe geographical patterns. Furthermore, some distinctions, such as facultative vs. obligate, involve both patterns and processes.

Within broadly defined flight types such as soaring, it seems that the internal state of the bird is roughly constant. That is, a soaring bird on a short flight or a long flight probably has similar costs in its energy budget and internal response to flight (Mandel *et al.*, 2008). However, flight distance can be influenced by many factors, including weather and navigation concerns, including responses to wind drift (Thorup, 2007), as well as trade-offs between map- and compass-based navigation (Nathan, 2008).

Here, we examine the relationship between migration patterns and response to external conditions in migrating Turkey Vultures (*Cathartes aura*). North American populations of Turkey Vultures include two subspecies that engage in a variety of migratory behavior (Kirk and Mossman, 1998). *C. aura septentrionalis* populations, which reside in the eastern United States, include birds that do not migrate, birds that migrate as far south as Florida, and

several intermediate migratory behaviors. In western North America where *C. a. meridionalis* dominates, most vultures appear to migrate longer distances, with large numbers of birds making an intercontinental migration to northern South America (Bildstein, 2006).

Given the variety of migratory behavior exhibited by this species, as well as the variety of weather conditions experienced by various populations, we set out to explore whether responses to external conditions could be characterized similarly for all migratory groups of vultures regardless of migration distance and path. We tagged birds from three sample populations: an eastern coastal population trapped near their breeding areas in Pennsylvania, a central-plains population trapped near their breeding areas in Saskatchewan, Canada, and a western coastal population trapped on migration in California. Vultures from Saskatchewan fly across the Great Plains, whereas the two coastal populations migrate along coastal mountains. The western and mid-continental populations migrate to Central and South America, whereas the eastern population migrates to Florida. As a null hypothesis, we suggest that different mean weather conditions (i.e. mean wind speed, turbulence intensity and uplift availability), together with geographic conditions along the coasts and the plains will lead to different patterns of observed movement, without a need to invoke different flight strategies. Observations suggest that vultures migrate using a few basic processes: soaring-gliding using thermals, slope-soaring using orographic winds, and flapping. Flapping is used only for very short movements and during landing and takeoff, and we will not explore it further here (c.f. Ferland-Raymond *et al*., 2005).

It is not possible with current technology to obtain meteorological observations during the flight time and exact flight path of migrating birds. Here, we address this problem by using a model-measurements hybrid dataset at a relatively high regional-scale of resolution (32x32 km), available through the North American Regional Reanalysis (NARR) (Mesinger *et al.*, 2006). This dataset is compiled using model-generated estimates of historical and present weather across a 3-dimensional grid, forced by observations from satellite and ground-based meteorological stations. These data have several advantages over interpolation of sparse direct measurements. First and most importantly, they have predictable error rates and a uniform distribution across the continent, making standardized comparisons over large spatial areas and time periods possible. The model also provides variables that are not typically measured by weather stations, such as turbulent kinetic energy (TKE) and surface heat flux. For studies of soaring flight, the most useful of these are estimates of both turbulence and vertical movements of air. Model-derived data also have limitations that measured data do not. Because they are calculated, they are prone to input errors and biases in the model. The North American Regional Reanalysis has a fairly high error rate in measuring precipitation (Mesinger *et al*., 2006), for example, because rain gauges often have poor temporal resolution. The strength of the resolved vertical air movements is highly dependent on the choice of the spatial resolution of the model. Therefore, at a resolution coarser than a few km^2, variables that are strongly dependent on vertical wind, such as heat flux, frictional velocity, and TKE must be parameterized using empirical-mechanistic schemes. The choice of a particular parameterization scheme can lead to model bias. In this study, because of the large spatial and temporal scope, we concluded that the

benefits of calculated variables (standardization and large scale of inference) outweighed their costs (potential bias, larger error and dependency on model characteristics).

We chose to examine migratory movements in the context of the Movement Ecology Framework (Nathan *et al.*, 2008; Mandel *et al.*, 2008). Here, we look at the role of **external effects** on **movement,** and **navigation** at a single spatial and temporal scale. Despite the fact that migration encompasses a range of scales, we are interested primarily in the mechanics of migration and, therefore, we focused on the smallest temporal scale available to us, hourly. **External effects** were characterized by the aforementioned weather variables and by topography, using a USGS digital-elevation model to calculate terrain ruggedness (Riley *et al.*, 1999). For statistical purposes, we define **movement** as the straight-line distance between two observed locations measured on the vulture separated in time by one-hour. **Navigation** is defined according to angular deviations in hourly tracks from the overall linear bearing of the seven previous tracks (see Mandel *et al*., 2008).

We used migration paths from 11 GPS-tagged Turkey Vultures to address the question of how soaring birds respond to changes in landscape and weather conditions. We explore the flight strategies by which a soaring bird completes a long-distance migration by measuring the relations of observed patterns of movement to weather and landscape. Such an understanding will facilitate predictions about potential changes in movement patterns as a result of climate change, as well as understanding why Turkey Vultures, alone among vultures, regularly undertake long-distance migrations.

Methods

Time series of movements were obtained by tagging vultures with solar-powered GPS units, with a spatial resolution of <10 meters, that uploaded their data to satellites. These tags record locations hourly. Birds were tagged in Pennsylvania, Saskatchewan, and Southern California from 2004-2008. For this analysis, only the 2 months of peak southbound migratory movements were used (October and November), and these data were used only in birds which showed latitudinal movements that exceeded the range of latitudinal movements displayed during breeding and wintering periods. This criterion produced the operational filter that only hourly movements >4 km were considered as migratory movements and included in this analysis. We termed the collection of all movements for a bird in a given fall migratory season as a "migration", and the migratory dataset included 11 individual birds over 15 different migrations.

In Pennsylvania Turkey Vultures were captured in padded leg hold traps that had had one spring removed and foam-tube padding added and were baited with carcasses of road-killed deer (*Odocoileus virginianus*) and groundhogs (*Marmota monax*). Traps were monitored from a blind, and birds were removed from traps immediately upon capture. In Saskatchewan, birds were hand-grabbed on their nests in abandoned farmhouses. In southern California birds were trapped in a large box trap baited using various small mammal carcasses as bait.

All birds were fitted with a solar GPS transmitter (Microwave Telemetry, 70 grams) using a "backpack"-style sewn harness of Teflon ribbon. Harnesses were sewn with unwaxed dental floss, which naturally rots after several seasons (E. Henkel, pers. comm.). Captured birds were offered dead mice

while in captivity, and all were released within 24 hours. Birds preened vigorously immediately after release, but there was no noticeable effect of tagging after 2-3 days.

Assembly of database: We assembled hourly-movement vectors coded in radial coordinates from the GPS movement data. Radial coordinates have the advantage of (a) uncoupling the strong correlation of movements in the X and Y direction in both movement and wind speed, (b) properly weighting large changes in direction on small movement days, and (c) conceptually separating the ability to fly long distances from the direction of flight. In radial coordinates, it becomes necessary to establish a principal axis of movement, and to measure angles (of both wind direction and movement) in terms of deviations from that axis of migration. In addition, the interaction of wind speed and direction becomes a critical measure for interpreting the appropriate effects of wind.

Because the movements examined consisted of multiple legs with different dominant bearings, we did not choose a single axis of migration for all points along the migratory journey. Instead, for every movement vector, we used the bearings of the previous seven movement vectors to establish a direction of movement; we term this the local axis of migration. We then took the absolute value of bearing of the movement vector minus the local axis of migration; we termed this the bearing deviation. Wind direction was calculated in the same way, as a bearing minus the local axis of migration, which we termed wind deviation. Thus, a wind deviation of zero would be considered a tailwind, whereas a wind deviation of 90 degrees would be a perpendicular crosswind. Following Oliveira *et al.* (1998), we used bearing and wind deviations to fit

linear models. All angle calculations were done using the “Circular” package in R v. 2.3.1 (Ihaka and Gentleman, 1996; Lund and Agostinelli, 2007).

Time Series: We used ARIMA techniques (Box and Jenkins, 1970) to estimate the appropriate covariate structure, which was subsequently applied to all models. ARIMA is a methodology to diagnose trends, autoregressivity, and sampling error in a time series dataset, and then to compensate for the presence of any of these using differencing, autoregressive correlation structures, and moving-window averaging, respectively. In all cases, a correlation matrix with a single autoregressive component was deemed appropriate and was applied to all dependent variables. In essence this meant that our statistical null model was a correlated random walk.

Predictive Variables: We examined four classes of variables: present location of the bird, landscape, winds, and vertical air movement or turbulence (Table 4.1). We feel that these categories correspond roughly to what a soaring bird can perceive in flight: they know something about where they are, they can view the landscape below them, they can perceive horizontal winds, and they have some knowledge of vertical air movement (whether through feeling turbulence, seeing thermal-circling movements of other birds, or observing clouds). Although we were not able to measure directly the same information the bird perceives, we used model-derived variables that approximate these categories. Because variables within categories have a high degree of cross-correlation, only 1-2 variables per category were used in statistical analyses.

Table 4.1. Listing of variables by category. Doubly starred entries (**) were used in statistical analysis. The height of the planetary boundary layer (HPBL), despite being an atmospheric variable, was strongly correlated with terrain ruggedness, and therefore was included in the analysis as a landscape variable.

Present State	Landscape	Winds	Air moving vertically and Turbulence	
**Bearing Deviation OR distance (by model)	Terrain Ruggedness	**Wind Direction	Surface Heat Flux	**Turbulent Kinetic Energy (TKE)
Latitude	**HPBL	**Wind Speed	Vertical Velocity of Pressure Levels	Convective Available Potential Energy
Speed			Height of Cloud Top	Height of Cloud Top
Altitude				W*

Present location - The speed of travel and flight altitude measured at the start of the movement vector.

Landscape. – We used the GTOPO30 digital elevation model (DEM) available from the EROS database at the USGS, which has grid spacing of 30 arc seconds (~1 km). We created a map of terrain ruggedness based on the variance in altitude of adjacent grid cells using Manifold v. 2.1 (CDA International; www.manifold.net). Terrain Ruggedness was calculated according to the formula provided by Riley *et al.* (1999), and provides a unitless index of variance in elevation.

Horizontal wind and vertical air movements – Weather variable values were taken from the National Center for Environmental Prediction (NCEP) North American Regional Reanalysis (NARR) dataset (http://wwwt.emc.ncep.noaa.gov/mmb/rreanl/index.html). NARR (Messinger *et*

al., 2006) is a product of the ETA regional model (Janjic, 1994) forced with a large set of satellite, surface and balloon observations. It consists of a 3-dimensional grid that covers North America with a horizontal resolution of 32x32 km, a vertical resolution defined along pressure levels, and a temporal resolution of 2 minutes. Snapshot and time averaged data are saved every 3 hours.

The bird's longitude and latitude were matched with the nearest NARR grid-cell center. NARR data for that cell were interpolated linearly in time to the timestamp of the bird GPS data point. For 3-dimensional variables, we interpolated vertically using the NARR pressure level height variable (HGT; i.e. geopotential height) closest to the GPS-determined altitude of the bird. Four groups of variables were included: (1) Wind speed and wind direction, processed from the NARR variables for latitudinal and longitudinal wind velocities (UGRD, VGRD, respectively). Horizontal winds were translated into polar coordinates, and the angle was translated into a deviation from the local mean direction of movement.; (2) Turbulent kinetic energy (TKE) was parameterized using empirical relationships between surface fluxes and the stability of the atmospheric boundary layer (ABL) (Mellor and Yamada, 1982). High TKE is typical for days with intermediate wind levels and strong convective heat flux from the ground (i.e. cloudless hot days), and indicates the presence of strong thermals; conversely, days with very strong winds, neutral boundary layer conditions and strong mechanical shear can produce high values of TKE (referred to here as "shear" TKE; Stull, 1988). (3) Pressure vertical velocity (VVEL) is defined as the rate of change over time of the height of the pressure levels, which make up the vertical dimension of the grid. The vertical movement of pressure surfaces is associated with the daily cycle of

ABL dynamics and mesoscale pressure fronts. (4) Cloud-top height, a two-dimensional model field (HGT:cld top), indicates the strength of parameterized convective activity in the ABL. In addition, we used sensible heat flux (SHF), which is a measure of energy flux from solar radiation along the earth's surface, and calculated W*, the free convection scaling velocity, as potential indications of uplift.

We specifically tested the correlation structure within vertical air movements and turbulence category (Figure 4.1). Here, we had an array of variables, all produced from parameterization schemes within the NARR. Although a variable such as W*, the free convective scaling velocity (Stull, 1988), which seems to directly capture vertical air movements at a scale appropriate to birds, is conceptually most appropriate, the high degree of parameterization involved in calculating this variable ultimately yielded a poor fit to the data. Similarly, variables relating to cloud height might seem most appropriate perceptually, as it is something the bird could see, but does not correlate precisely with available convection for flight. Of the variables listed in Table 4.1, turbulent kinetic energy (TKE), indicating the kinetic energy of the mixing of air within a bounded area in the model, yielded the best predictive power, and was used in our analysis. Height of the planetary boundary layer (HPBL) was correlated with TKE but represents a larger scale phenomenon, and so was included. Direction and speed of winds were also included. Terrain ruggedness contained a high degree of correlation to TKE and HPBL. HPBL, which had only weak correlations with other vertical movement variables and had a significant effect on movements, was therefore included in the statistical models as a landscape variable and terrain ruggedness was omitted from the analysis.

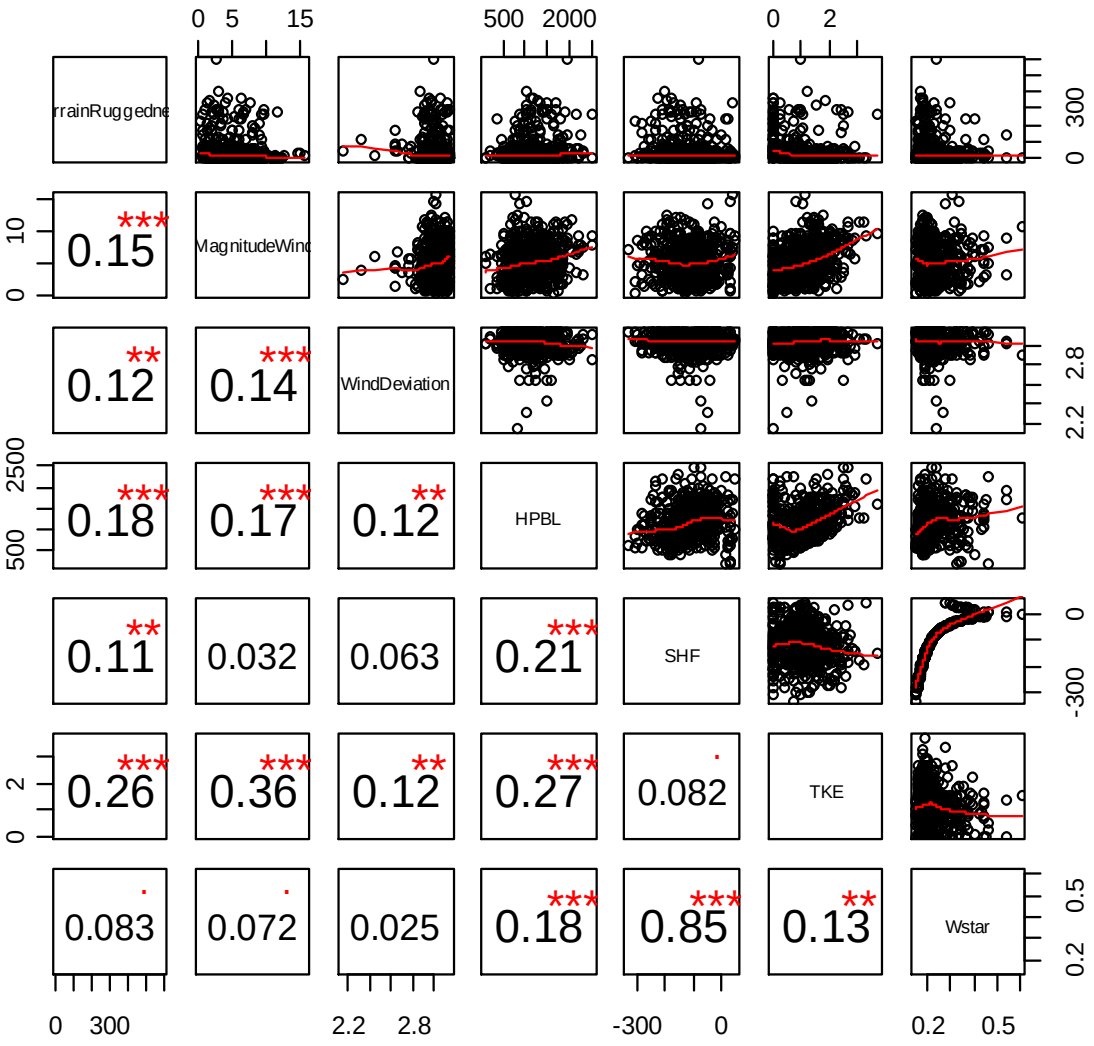


Figure 4.1. Correlation matrix of major variables explored before statistical modeling. The upper right diagonal contains scatterplots and smoothed trend-lines, while the lower right diagonal contains correlation coefficients (r-values) and stars representing significance (***:p<.001, **:p<.01, *:p<.05).

Model simplification

Statistical analyses consisted of mixed-linear models created using the "nlme" package in R (Pinheiro *et al.*, 2007) with either the log of each bird's movement distance or navigation bearing as the dependent variable and all

other external and present location variables as independent variables. For each mixed model, an *a priori* correlation structure from ARIMA analyses was specified with a single degree of autocorrelation. All models began with the inclusion of all main effects and all potentially relevant interactions. Backward selection, on interactions first, using maximum likelihood, was performed to determine the final model. Final models were compared with initial models using ANOVA, and AIC was observed to decrease throughout model selection in all models. Parameter values were then estimated using restricted maximum likelihood. The models were compared to identical models without random effects, to determine if the random effects significantly changed the model. This was done by comparing the difference of -2(ln-likelihood) with a chi-square table and 1 degree of freedom.

Results

The full migratory data set is mapped in Figure 4.2. Three east coast vultures flying from the Northeastern US to Florida traveled along a route that included both coastal lowlands and Appalachian mountains. Five continental-interior vultures, flying south from Saskatchewan, traveled through the central plains of southern Canada and the central United States and did not encounter mountain ranges until they had reached southern Mexico, where they joined the migratory route of the western population along the central Cordillera of that country. Three West Coast vultures traveled along Pacific Coast mountain ranges while flying south through California, Mexico and Central America, and into northern South America. Thus, from the perspective of terrain encountered, it is possible to view the east and west coast migrants, both of which traveled along mountain ranges, as more topographically similar

than mid-continental migrants, which did not fly along mountains, at least during the large migration section through the United States and Canada.

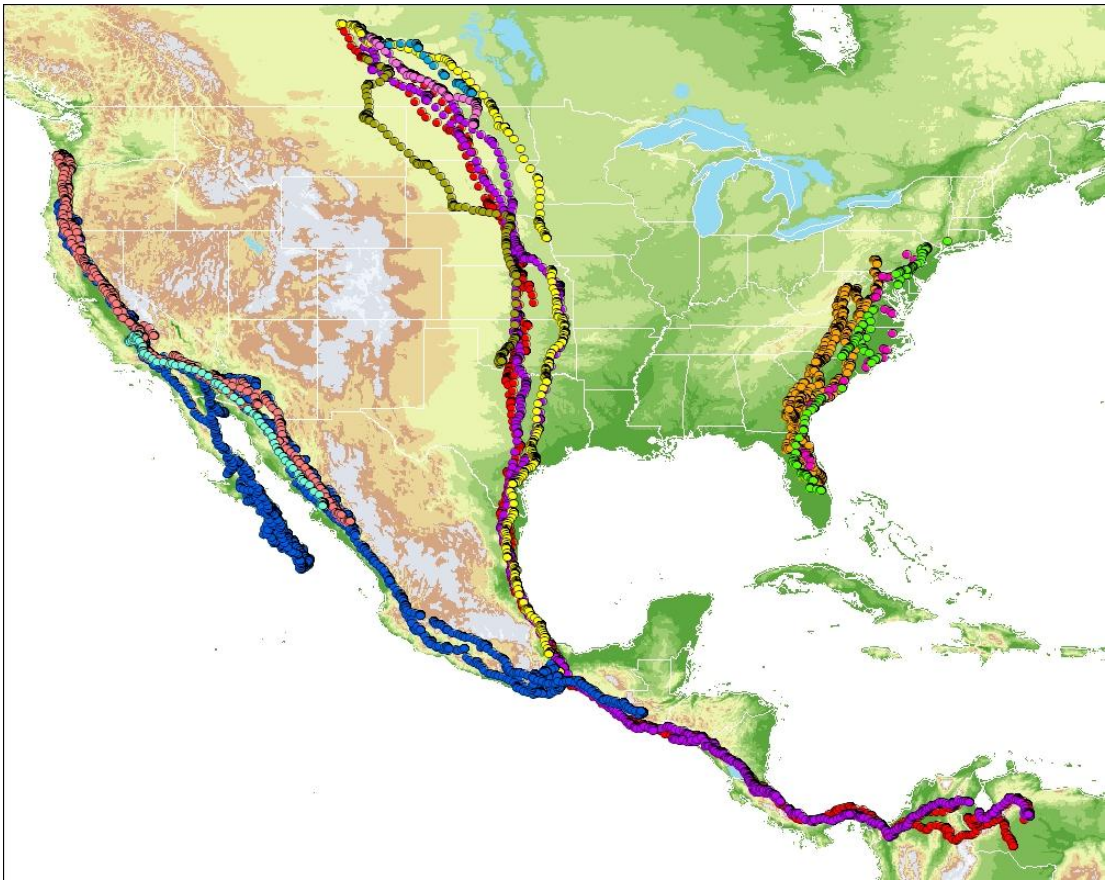


Figure 4.2. Map of complete vulture movements. One movement per day is plotted. Nearby migrations are plotted in different colors.

Given this difference in landscape, it was not obvious if the birds would use the same weather and landscape features to enable movement during migration. Table 4.2 shows the final models for movement. As in Mandel *et al.*, (2008), TKE was most strongly correlated with movement in all populations. However, it also is clear that the movements of east and west coast birds, which fly over and along mountains, are influenced by the height of the planetary boundary layer. In both populations, a higher planetary boundary

layer reduces the positive effect of TKE (Figure 4.3). For mid-continental birds, which are primarily flatland migrants, the height of the planetary boundary layer did not affect movement. For these migrants, winds that deviated from the primary axis of movement were correlated with shorter distance flight.

Table 4.2. Summary of model effects for Distance model. 0 means that a variable was eliminated from the final model, whereas a + or - indicates its inclusion and the direction of the effect. *=p<.05; **=p<.01; ***=p<.001.

Effects	**East Coast Birds**	**Mid-continent Birds**	**West Coast Birds**
TKE	+,***	+,***	+,***
HPBL	0	0	0
Wind Direction	0	-,**	0
TKE*HPBL	-,**	0	-,**

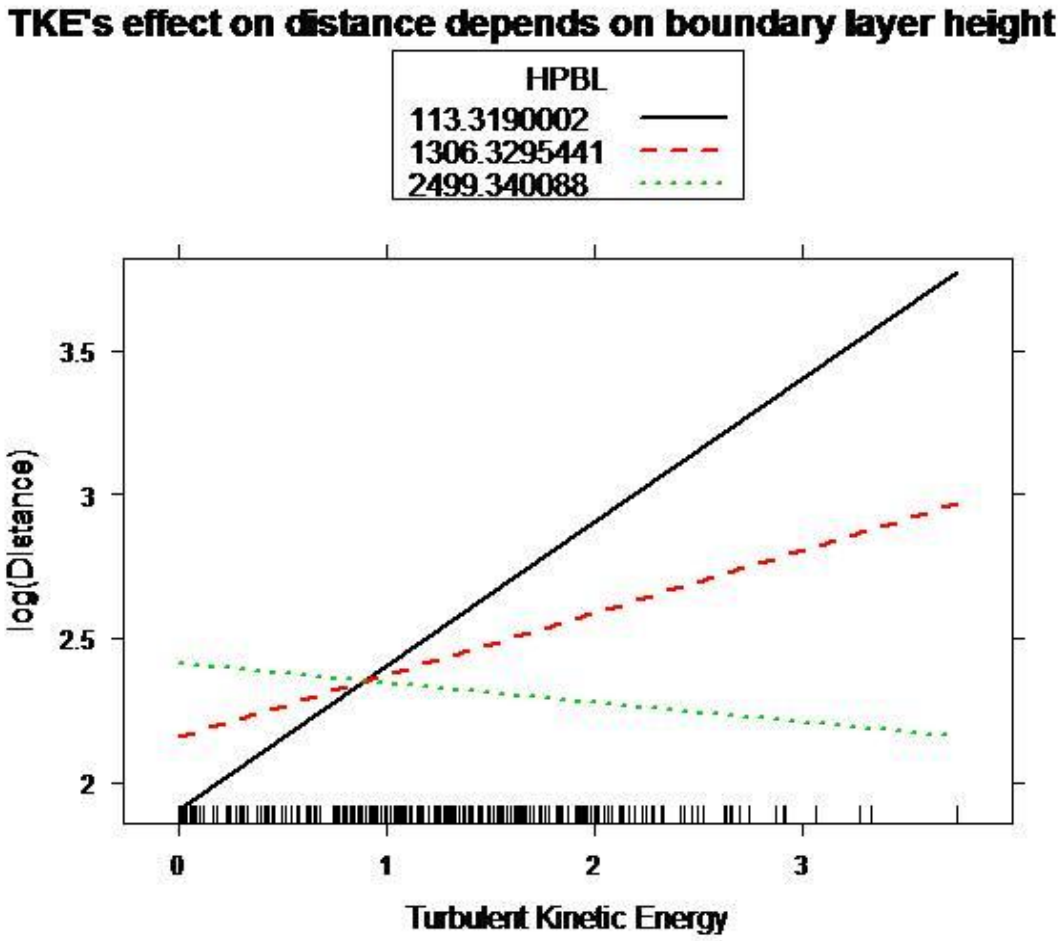


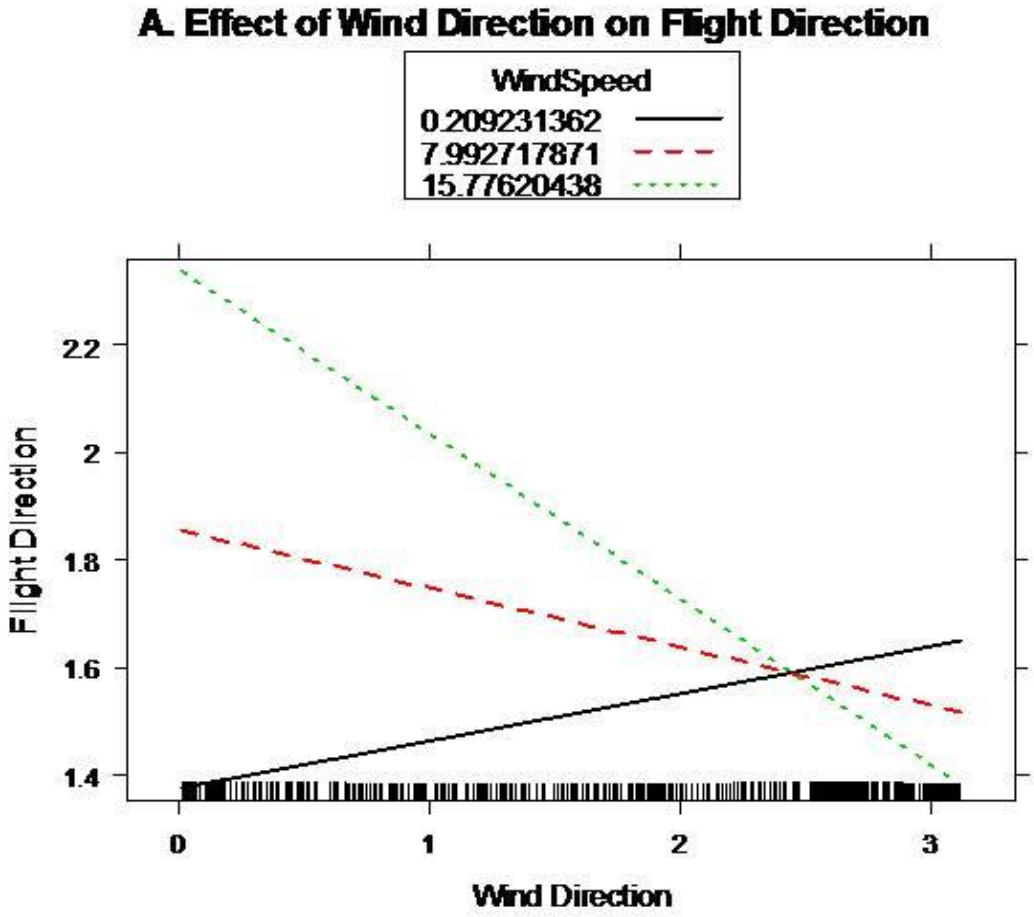
Figure 4.3. Interaction plot from the distance model of the eastern population. Each colored line corresponds to a specific value of planetary boundary layer height (in meters), which can roughly be seen to represent the maximum height achieved by surface convection, with black corresponding to the lowest planetary boundary layer height, and green corresponding to the highest. The relationship is similar for the West coast population, and shows that TKE promotes movement at low levels of HPBL, but matters less when the planetary boundary layer is high. This suggests that, at high levels of HPBL, other movement options, such as slope-soaring, that do not depend on TKE the way it is parameterized in the model are being used.

The navigation models revealed similar patterns. For all populations, horizontal wind speed had the largest role in determining the extent of deviations from the principal axis of movement (Table 4.3). However, the way in which winds interacted with navigation varied by population. For continental

interior migrants, the pattern was simple. High-velocity crosswinds led to course deviations, and this effect was stronger with higher winds. No other factors influenced flight direction in this population. For the west coast birds, high winds were positively correlated with long-distance movement regardless of their direction. The positive role of winds in this population likely indicates the use of slope soaring along mountain ridges, a method that is dependent on strong, steady coastal winds. The height of the planetary boundary layer was negatively correlated with navigation. As the boundary layer is elevated along mountain ridges as the surface increases in height, this also fits the pattern that these birds are slope-soaring along the mountain ridges; when they find themselves in a place with a high boundary layer, they might be changing direction to follow mountain ridges. East Coast birds reacted to wind speed and direction in a way that also suggests slope soaring. In low winds, regardless of direction, birds maintained course. In high winds, however, bearing deviation was lowest as winds approached a perpendicular angle to the birds' direction. Given the geography of the region, with migration paths and the Appalachian range aligned on a North-South axis and sea-breezes providing a strong and regular easterly wind, this pattern suggests slope-soaring. High winds in the direction of movement caused course deviations, which is likely a result of disrupting the spatial structure of TKE (Mandel *et al.*, 2008). Figures 4.4a and b shows the contrasting effect of wind strength and direction between the east coast and mid-continent vultures.

Table 4.3. Summary of effects for Bearing models. Symbol definitions are the same as in Table 4.2.

Effects	East Coast Birds	Central Birds	West Coast Birds
Wind Deviation	0	0	0
Magnitude wind	0	-,*	+,***
HPBL	0	0	-,*
Wind Deviation * Magnitude Wind	-,*	+,*	0



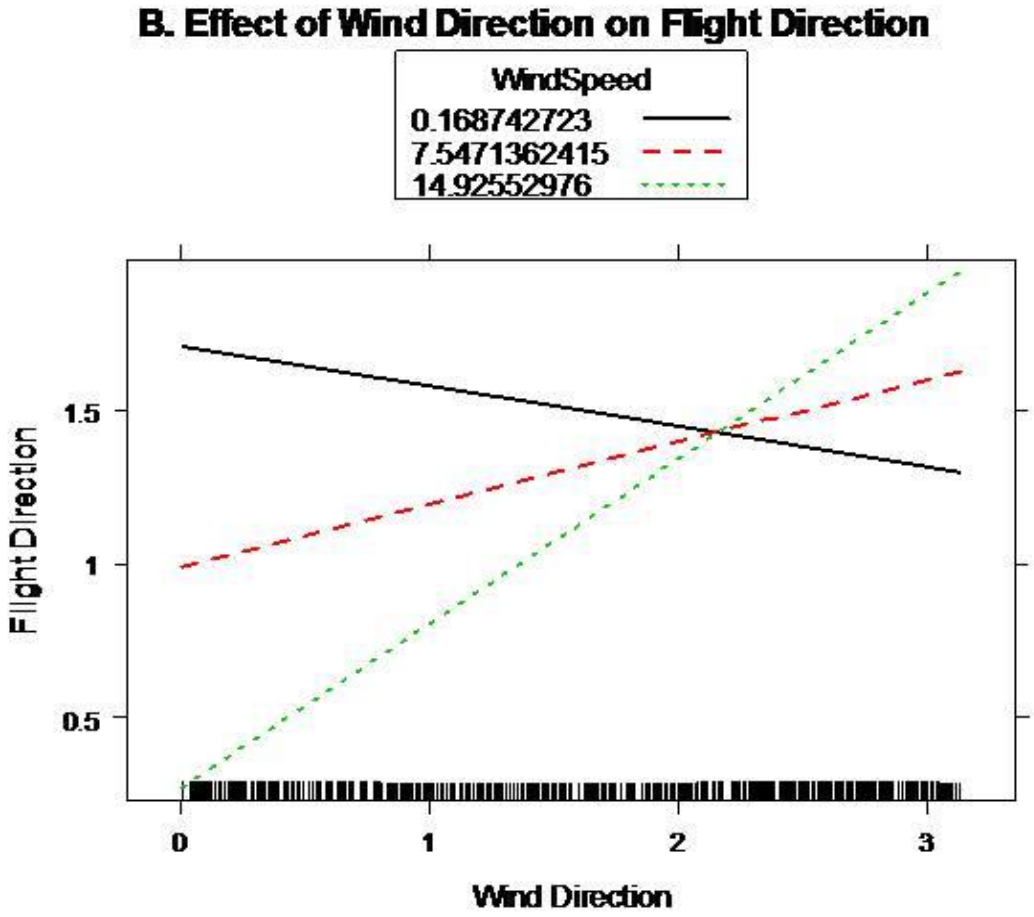


Figure 4.4. The contradictory role of horizontal winds in the navigation of east coast (A.) and mid-continental (B.) birds. Lowest wind speeds are represented by a black line, and highest wind speeds are represented by a green line. The effect of wind direction on bearing is shown at the average wind speed for each line color. It appears that east coast birds are using slope soaring at times during migration, whereas the mid-continental birds, without a dominant mountain range to deflect the wind, are being blown off course by similar winds, and must compensate for wind-drift.

Discussion

This analysis shows a remarkable similarity in response to landscape and weather among geographically and behaviorally (in terms of overall migration length) distinct populations of Turkey Vultures. In all three populations, turbulence, represented here by the NARR model variable TKE, is the

dominant correlate of movement. This pattern is consistent with a flight strategy that is dominated by thermal soaring.

We also found evidence for an important slope-soaring component in migration among the two coastal populations. In these populations, at low boundary layer heights, motion is driven primarily by TKE, but in situations where the boundary layer is high, this effect disappears. Since boundary layer heights are known to increase in the presence of mountains (Lieman, 1993), we attribute this effect to a transition from thermal- to slope-soaring when the birds are traveling along mountain ridges. This transition does not occur in the interior, where migrants do not encounter mountains and the opportunity for slope-soaring. Interior migrants also are constrained by horizontal winds; the broader geographic heterogeneity and the availability of an alternate method of locomotion likely help minimize these effects in the coastal populations.

Differences in effects on flight direction are striking among the three populations. Our models suggest that each population has its own suite of navigational responses to weather. With respect to winds, several key differences emerge. Continental interior migrants, who migrate over relatively flat terrain, have a pattern that closely matches the null hypothesis – travel with the mean wind direction. Because of this, we attribute the changes in response to wind from the two coastal populations to the presence of mountains. West Coast birds show larger deviations in high winds and are not affected by wind direction. Instead, they migrate along the straightest path when the planetary boundary layer is high. East Coast birds fly their straightest paths either when winds are low or when winds are high but wind is orthogonal to the axis of movement, indicating a greater alternation between slope soaring and thermal soaring than occurs in West Coast birds.

As our movement ecology model demonstrates, the two coastal populations use both slope-soaring and thermal soaring, and therefore have more complex relationships to external conditions than do the continental interior migrants. Why the plains migrants do not follow a more direct route over the Rocky Mountains remains to be determined. One hypothesis is that their current route keeps them within the contiguous breeding ranges of Turkey Vultures, and thus allows for activities such as social foraging and communal roosting during migration. Another hypothesis is that the leading westerly wind direction in the eastern United States results with wind directed down-slope on the eastern face of the Rocky Mountains, which is not conducive to slope-soaring.

Disentangling different modes of flight and the conditions under which they are used should be a topic of future research. Our current approach successfully identified the signature of behavior in the relationships between migration paths and weather variables. Our approach, however, is limited by the differences in scales between particular behaviors and conditions during flight (at the very small scales), the resolution of the observations of movement (intermediate scale), and the larger regional scale at which spatially and temporally continuous meteorological data are available. With regards to time-scale; with a full hour between readings, both slope soaring and thermal soaring can take place. In addition, at an hourly time-scale, the signatures of these behavioral patterns on routes are less apparent In space because regional models operate at a multi-kilometer scale, and because parameterized variables, such as TKE and HPBL, are indicative of thermals but, at these resolutions, the models cannot directly resolve them. Nonetheless, the use of a regional atmospheric model to derive data on environmental conditions provided advantages not available with other

approaches: in no other way could we, for example, compare in a standardized way the physical environment of a bird in tropical Mexico with one in Northeastern Pennsylvania. It also allowed us to look beyond standard sparse measurements of mean wind and temperature and begin to understand the role of turbulence regimes, heat fluxes, and weather-landscape interactions in migratory movement.

Here, we are able to show that vultures employ different strategies based on the environmental circumstances they encounter, and that the effects of weather and landscape can interact with flight paths in complex ways. The topography of landscapes over which a bird flies matter at least as much as the winds and turbulence immediately around the bird, and these, in turn, interact to affect the spatial structure of thermals and the existence of updrafts. The end result of these interactions is one of the longest soaring migrations in the world, and the only long-distance migration by a scavenging raptor (Bildstein, 2006). Two principal migratory strategies emerged from this analysis: slope-soaring and thermal soaring. We found that landscape matters more than migratory distance in predicting which strategy is employed. The picture that emerges is that Turkey Vultures are able to switch between flight strategies as conditions merit, and it is interesting that the two coastal populations, in different subspecies, had migratory strategies more similar to each other than did the plains population and the west coast population, to which its members are presumably more closely related.

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CHAPTER 5

MOVEMENT ECOLOGY DURING THE ANNUAL CYCLE OF A MIGRATORY BIRD

Mandel JT, Bohrer G, Winkler DW, David Barber, Houston S, Bildstein KL

Abstract

A migratory bird's year can be divided roughly into four periods: spring migration, breeding, autumn migration, and over-wintering. In each of these periods, a migratory bird encounters distinct weather conditions. Based on observations and satellite tracks, it is clear that movement distances, path deviations, and levels of flight activity vary throughout the year. In North American Turkey Vultures (*Cathartes aura*), which depend heavily on soaring for their in-flight movements throughout the year, migrations consist primarily of directed movements with intermittent foraging; the summer period is dominated by home-range anchored activities that coincide with breeding; wintering, during which migrant Turkey Vultures join the roosts of southern residents, likely lacks both the directed movements of migration and the tightly anchored home range that accompanies breeding.

We set out to describe differences in movement and weather use by soaring birds related to these four periods. We found that path lengths, bearing deviations and activity periods varied by season in consistent and predictable ways. Autumn movementswere characterized by the longest hourly distances traveledand the smallest turning angles. Springmigration was accompanied by an increase in time spent actively moving daily. Winter and summer were characterized by shorter path lengths, higher turning angles, and a smaller amount of time spent flying. During both migratory periods, birds

responded to horizontal winds and thermals similarly, suggesting that most in-flight movement consisted of a combination of slope and thermal soaring. Navigation was influenced by the presence of turbulent kinetic energy (TKE). During the over-wintering period, birds did not adjust paths based on the weather variables tested, whereas in summer, when birds are foraging for both themselves and their young, paths were influenced by TKE and horizontal winds. Winter is likely to be the period of lowest-energy expenditure period for the birds we tracked.

Introduction

The annual cycle of a northern temperate-zone migratory bird can be divided into four distinct periods: spring migration, breeding, autumn migration, and over-wintering (Newton, 2008; Dingle, 1996). Raptors spend up to 40% of their annual cycle in migration (Newton, 2008), and including migration as a major part of this animal's life cycle seems sensible. Each of these periods are distinct in landscape and weather (i.e., temperate vs. sub-tropical and tropical) and biological motivation (i.e., breeding, feeding developing young, molting, pre-migratory fattening; Newton, 2008; Bildstein, 2006; Dingle, 1996). During autumn migration, birds travel from their breeding grounds to their wintering grounds, motivated primarily by a need to find a consistent source of food (Gauthreaux, 1982) during the temperate-zone winter, and, except in special circumstances such as crossing the Sahara (e.g. honey buzzards, Hake *et al.* 2003) or water crossings (Bildstein, 2006), are not necessarily temporally constrained. One might expect energy-minimization to be a priority over time-minimization during this period (Hedenstrom and Alerstam, 1995), and

weather effects and landscape use should reflect energy-minimization rather than time-minimization (Fuller *et al.*, 1998, Kjellen *et al.*, 2001).

Spring migration, on the other hand, involves a reversal of destinations, although in many cases the path differs from the autumn migratory path (Newton, 2008; Alerstam *et al.*, 2006; Bildstein, 2006), possibly because of adaptive wind-drift (Alerstam, 1990). The biological motivation is a return to the breeding grounds to breed or, in the case of communally nesting species, to help raise young (Newton, 2008). Often there is a strong time constraint in this migration, either to successfully synchronize breeding with a temporally brief increase in food supply, because of reduced food availability en-route, or to aid in competition for mates and nesting territories (Winkler, 2005; Visser *et al.*, 2004). In spring migration, one might expect time-minimization, rather than energy minimization, to be employed as a strategy for at least some parts of the migration (Hedenstrom and Alerstam, 1995), as there is strong competition for breeding territories that is expressed through time of arrival (Bildstein, 2006). In both autumn and spring migration, one would predict from these hypotheses that movement tracks would be longer and more directional than movements during breeding or over-wintering. In terms of response to external factors, we would expect movement to be heavily dependent on weather features in autumn migration. During spring migration, we might expect movement to be heavily dependent on weather features whereas, navigationally, migrants would sometimes favor a more direct route to the breeding grounds at the expense of optimizing the route for use of weather conditions or landscape features.

The other two major periods of a migratory bird's life do not involve long-distance, directed movement. However, they do occur in different latitudes and

landscapes, and are characterized by different motivations. During the summer breeding season, breeders are generally anchored in one geographic location, and most movements are likely devoted to foraging (Dingle, 1996; Houston *et al.*, 2008). And even non-breeding birds are less likely to change home-ranges during this period; birds tend to return to a location after natal dispersal year after year (e.g. swallows; Winkler *et al.*, 2004), and might begin the process of locating and competing for competitive breeding areas prior to their first breeding attempt. The movement behavior of many individuals during this time could be considered “station keeping” (Dingle, 1996), regular movements within a home range. On the wintering grounds, birds do not have a nest to anchor them geographically, nor do they have nestlings to feed. Birds must compete with local residents, who already have established home ranges and roosts (McGrady MJ *et al.*, 2002; Rappole *et al.*, 1989). Therefore we might predict that migratory birds will be least responsive to weather and terrain during the breeding period, when food is abundant and foraging demands high. During the wintering period, we might expect local terrain to play a role in navigation, since nomadic birds will spend a portion of their time exploring a new landscape, whereas competition, both with other migrants and local residents, may cause geographical shifts in food availability. The lack of an anchoring nest might also increase the frequency of exploring, finding and changing roost sites.

We can test the hypothesis that movement patterns are driven by differences in biological motivation at different times of the year by taking a detailed look at the relationship of movements to external state. If a bird’s response to weather remains constant while the weather itself is changing, then changes in pattern can likely be attributed to changes in the bird’s

environment. If, on the other hand, a bird's response to weather varies seasonally in addition to the weather itself changing, than changes in pattern are likely the result of both changes in behavior and changes in the bird's environment.

Here, we test these predictions in a migratory soaring bird, the North American Turkey Vulture (*Cathartes aura*). Using data collected via GPS-ARGOS transmitters over multiple years, we quantified the movements of Turkey Vultures across North America. Working within a Movement Ecology framework (Nathan *et al.*, 2008; Mandel *et al.*, 2008) we explored whether bearing deviations and path length varied by time of year to test the prediction that variations in biological motivation throughout the year would lead to different movement tracks. We then explored the role that the birds' reaction to external factors such as weather and geography had in motivating these different patterns.

Methods

Trapping and tracking of the vultures and assembly of database and variables used in this study are explained in detail in Mandel *et al*. (2008), as well as in Mandel *et al*. (Chapter 4, this dissertation).

We divided annual cycles into four parts by defining spring and autumn migration according the criteria laid out in Mandel *et al*. (2008): Autumn migration consisted of migratory movements during October and November, identified by historical hawk count data (Zalles and Bildstein, 2000) as the main time period of migration. During this period, latitudinal shifts of directed movements exceeded the minimum and maximum latitudes of June and July movements, and the birds ceased directed movement when they entered the

latitudinal range established in January and February. Spring migrations were calculated in the same way, using data from April and May, which is the major period for spring migration. Over-wintering was defined as the period between autumn and spring migration, and breeding as the period between spring and autumn migration. Although there are likely to be transitions in motivations at the ends of these time periods, such periods of transitional motivations likely represent a minor part of the data collected.

Our dataset consisted of the tracked movments of 14 birds during a five year period. We adopted a conservative filter for hourly scale analysis that consisted of a movement of at least 1 km, and during which both the beginning and end of each hour was successfully recorded by the GPS loggers (i.e. there are consecutive hourly measurements on the GPS that can bound an hour of movement). After filtering, there were 7,811 hourly movement segments for use from 2004 through 2008.

Statistics: To examine the patterns of weather effects, both hourly distance and hourly turning angles from spring, summer, autumn, and winter were treated separately as dependent variables against the following independent variables: wind speed, wind direction, height of the planetary boundary layer (HPBL), and Turbulent Kinetic Energy (TKE). Weather variable values were derived from the National Center for Environmental Prediction (NCEP) North American Regional Reanalysis (NARR) dataset. (http://wwwt.emc.ncep.noaa.gov/mmb/rreanl/index.html). NARR (Messinger *et al.*, 2006) is a product of the ETA regional model (Janjic, 1994) forced with a large set of satellite, surface and balloon observations. It consists of a 3-dimensional grid that covers North America with a horizontal resolution of 32x32 km^2, a vertical resolution defined along pressure levels of 25 hPa in the

lower atmosphere, and a temporal resolution of 2 minutes. Snapshot and time averaged data are saved every 3 hours. We interpolated linearly in space and time to the nearest grid cell and hour for each point. See Mandel *et al*. (Chapter 4, this dissertation) for detailed discussions of selection of variables, cross-correlations among them, and interpretation.

We examined two aspects of movement from each period: distance moved during consecutive hours, and turning angles measured as a deviation from the local axis of movement (Mandel *et al*., 2008) calculated from the previous seven hours of movement. For distance models, we log-transformed the distance distribution to satisfy normality assumptions. Analysis was done using mixed linear models in R (Pinheiro *et al*., 2007) with bird as the random effect, and with an auto-regressive correlation matrix. All models began with the inclusion of all main effects and all potentially relevant interactions. Backward elimination, on interactions first, using maximum likelihood and chi-square with a significance threshold of $p<.05$, was performed to determine the final model.

Descriptive statistics: Movement patterns within the four periods were described according to three criteria: the amount of time a bird was actively moving (>1 km) as a percentage of all recorded hourly periods, the average distance of such movements, and the average turning angle (measured as a deviation from the local axis of movement; calculated with the “circular” package in R). ANOVA’s were used to assess differences among these groups, and charts of Tukey’s Honest Significant Difference were used to find specific differences between individual groups.

Results

Each of the four seasonal periods had distinctive patterns of movement (Figure 5.1). The two migratory periods included more directional (i.e., straighter) and longer hourly movement legs than did the two non-migratory periods. That said, hourly movements during autumn migration were straighter than they were in spring migration, whereas the summer period had the shortest hourly movement legs. On the other hand, turning angles in summer did not differ significantly from those in winter and spring. When activity was examined, spring migration correlated with the highest amount of time in flight, whereas winter was the most sedentary (Figures 5.2a, b, and c).

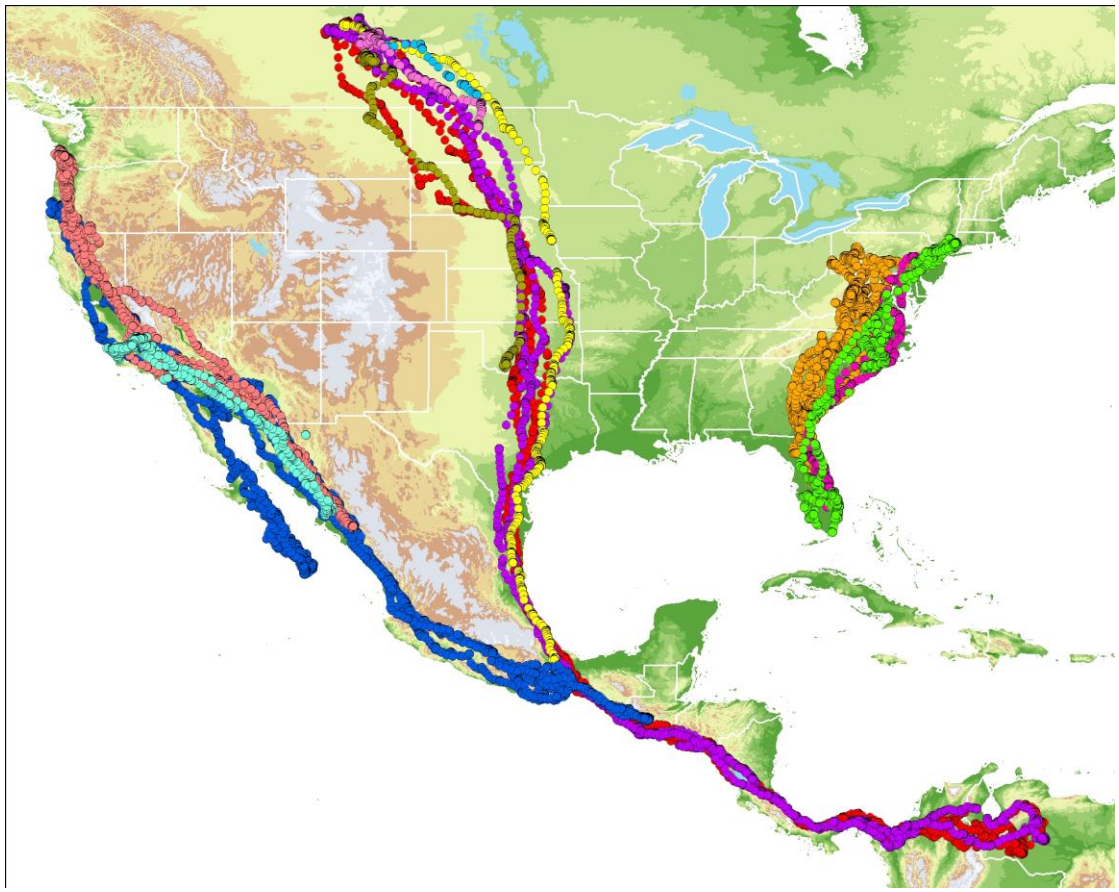

Figure 5.1. Color coded map of movements used in this study. Each bird is given its own color. Ground elevation is indicated on the map by the color of shading.

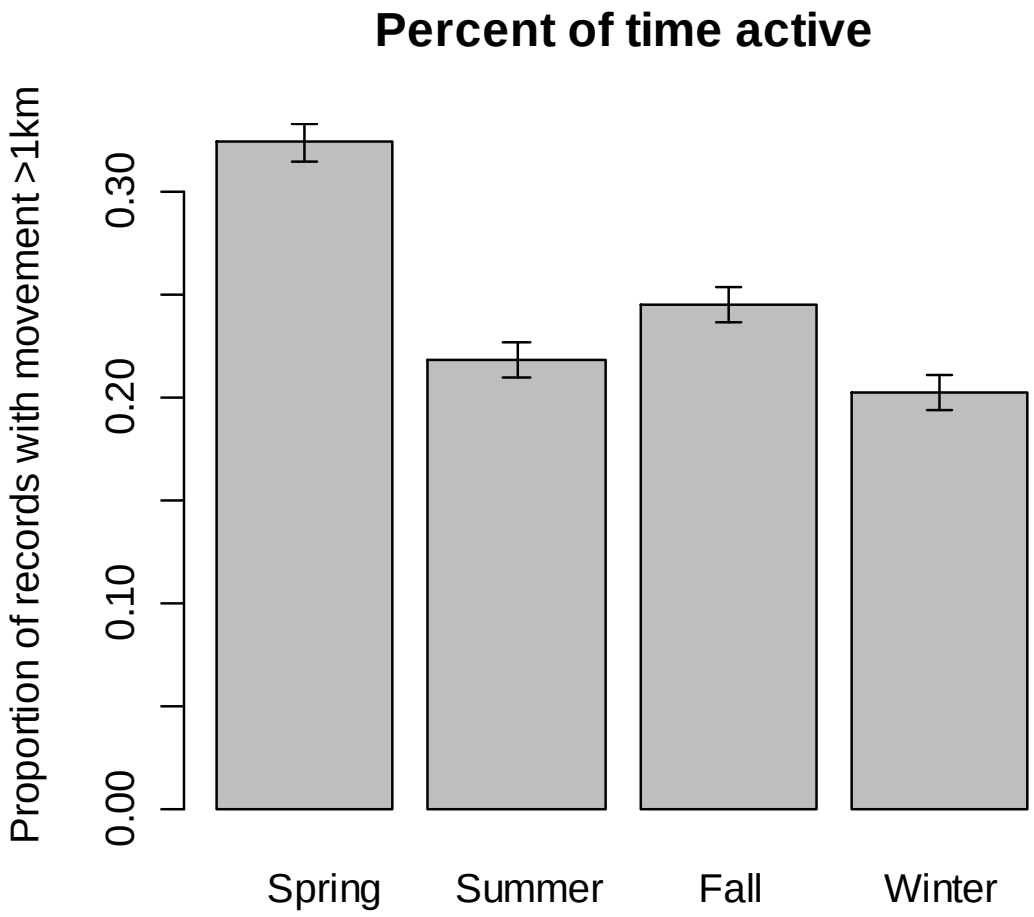

Figure 5.2a. Proportion of time that birds were actively moving (movement > 1 km/hr). Spring period contains significantly more activity (logistic regression, p<.0001). Contrasts tested with Tukey's test.

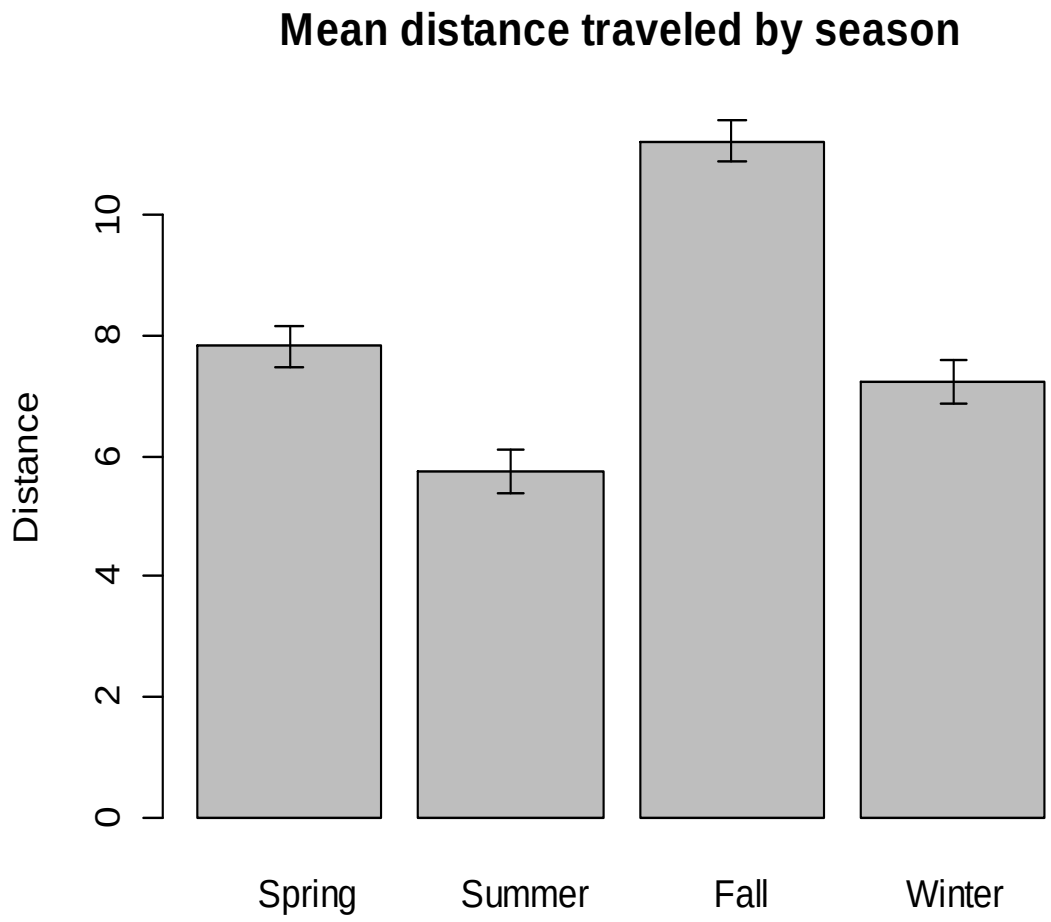

Figure 5.2b. Mean and standard error of distance by season. Distance is measured in km per hourly movement segment. Seasons were significantly different (ANOVA, p<.001, Tukey's Honest Significant Difference for contrasts).

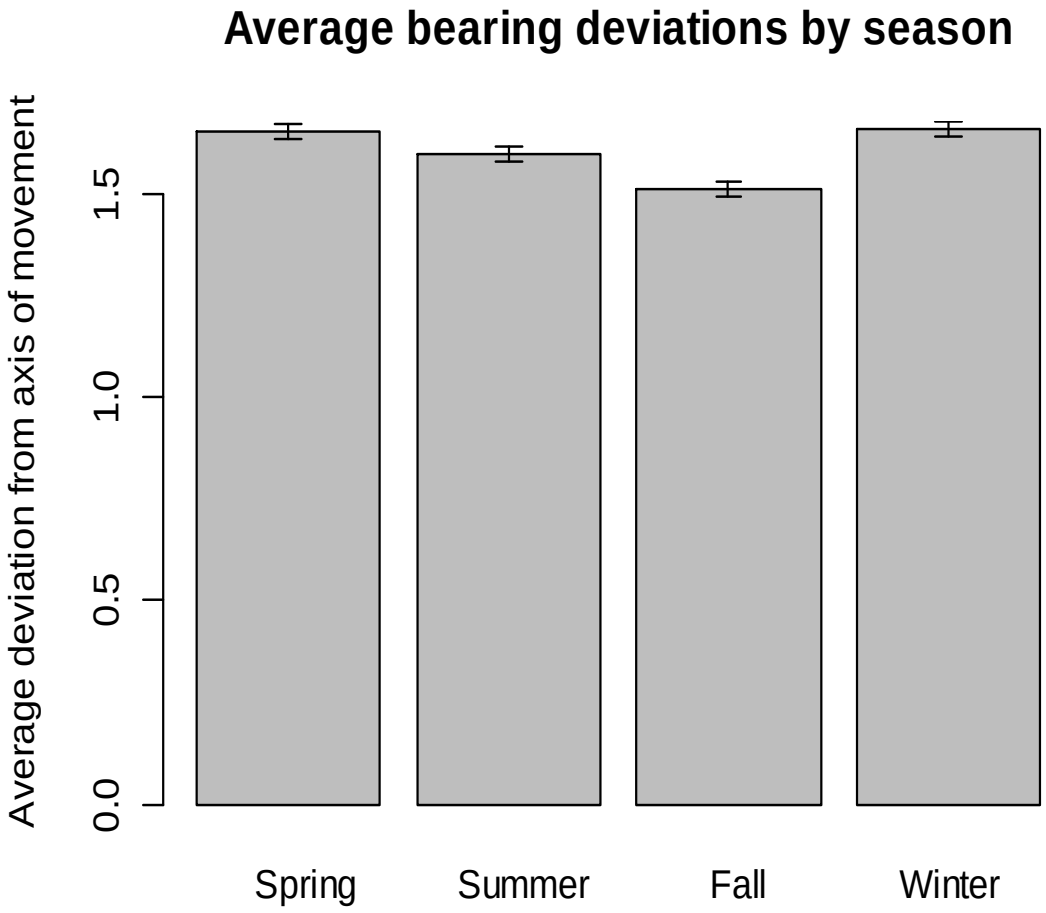

Figure 5.2c. Average bearing deviations by season. Fall is significantly different than all other groupings (ANOVA, p<.001; Tukey's Honest Significant Difference for contrasts).

In the analysis of weather effects, certain aspects of movement, such as the correlation between distance and the interaction of turbulent kinetic energy (TKE) with the height of the planetary boundary layer (HPBL), were constant throughout the year. In an analysisthat focused specifically on autumn migration (Mandel *et al*., Chapter 4), this interaction was interpreted as evidence of a flight strategy consisting of a combination of slope-soaring and

thermal soaring. In this interaction, the positive correlation between TKE and distance decreases at high boundary layer heights, as the bird switches from a thermal soaring strategy to a slope-soaring strategy. Wind speed was a significant negative correlate of distance only during the summer (Table 5.1a). Because of breeding, summer is the season in which short round trip flights are likely to be most common, as a result of servicing a nest, and thus escaping the negative effects of high winds by changing direction is likely to be less of an option.

TKE correlated with straighter movement paths in all seasons but winter, where none of the weather variables tested had a significant explanatory effect. As with the distance model and likely for similar reasons, wind speed mattered only during the summer season, when it had a negative correlation with path straightness that depended on wind direction.

Table 5.1. Factors influencing distance (A) and navigation (B) by season. A "0" indicates no significant influence in the model, while + indicates a positive effect and a – indicates a negative effect. *: p<.05; **: p<.01; ***: p<.001.

A. Effects	Spring	Summer	Fall	Winter
Wind Speed	0	-,*	0	0
TKE*HPBL	-,***	-,***	-,**	-,***

B. Effects	Spring	Summer	Fall	Winter
TKE	-.**	-,*	-,*	0
Wind Speed * Wind Direction	0	-,**	0	0

Discussion

Turkey Vultures vary their patterns of movement based on the time of year. Birds traveled longer distances and flew straighter paths on an hourly basis during the autumn migration. The patterns of weather effects during autumn, in

which increasing levels of TKE are correlated with increasing distances in a way that decreases as the height of the planetary boundary layer increases, suggest that at this time of year vultures used a combination of slope-soaring and thermal soaring (Mandel *et al*., Chapter 4, this dissertation), with the latter being particularly important. Vultures in all seasons flew straighter paths during periods of high TKE. They did not spend significantly more time actively moving than during winter or summer. The combination of a heavy reliance on weather and a relatively low amount of time spent moving suggests that energy-minimization is a likely variable being optimized during this migration (Hedenstrom and Alerstam, 1995).

An analysis that focused specifically on fall migration (Mandel *et al*., Chapter 4, this dissertation) finds similar patterns of weather effects, and also an effect of wind on navigation and, in mid-continental “plains” migrants, an effect of wind on distance. To ensure comparability of movements throughout the year in this analysis, we looked at all movements of at least 1 km; in previous studies that focused specifically on migratory movements, a distance limit of 4 km was used (Mandel *et al*., 2008, Mandel *et al*., Chapter 4, this dissertation). It is likely that the requirement in this study to look at movements more generally, rather than focusing solely on migratory movements, is responsible for the differences in weather effects between these two studies.

Spring migration consisted of shorter hourly movement legs than did autumn migration, and it had turning angles that were statistically indistinguishable from the summer and winter periods. Spring migrants, however, spent many more hours per day actively moving than at other times of the year. This spike in activity might be the cause of the shorter average distances and higher turning angles (i.e. the birds are willing to fly in sub-

optimal weather conditions). Alternatively, it might be a mechanism to compensate for these shorter distances, which are possibly caused by seasonally poor weather for long-distance flight. It also may be that they were less likely to stop and feed en route in spring than in autumn.

Observations from raptor watch sites show a much stronger signal of migration along ridges during the autumn than during the spring (Zalles and Bildstein, 2006). A willingness to fly in a broader range of weather conditions and a broader range of times, as our data suggest, could be one contributing factor to the more diffuse migration patterns observed during the spring at these locations. These increased activity rates suggest that that time rather than energy is being minimized during spring migration (Hedenstrom and Alerstam, 1995). In other species (i.e. Visser *et al.,* 2004), there is evidence that minimizing the time of spring migration can play an important role in successful breeding.

During the summer, vultures had the shortest average movements, turning angles comparable to winter and spring and rates of activity similar to winter and fall. Summer was also the only season in which winds had an effect on movement. High wind speeds were associated with shorter distances and higher turning angles, although this second effect was moderated by wind direction. The summer is the breeding season for Turkey Vultures, and the need to return often to nest sites likely anchored their movements in a way that did not happen at other times (Dingle, 1996). This behavioral constraint is likely the cause of both the shorter movement distances and of the effect of wind on movement. Birds that are not changing roosts, and must return to a nest frequently, are more likely to take short trips when possible, since all outbound movements will be accompanied by a return movement. Winds are

likely to have an effect on movement during this season for the same reason: if all movements are round-trips, it becomes much harder to compensate for or avoid winds from any given direction for both the outbound and inbound legs of a trip.

During winter, birds moved longer distances than during summer, but shorter than during migration periods. Turning angles were similar to those recorded during spring and summer, and activity rates were similar to those in autumn and summer. As in all other seasons, the pattern of weather effects suggests that birds used a combination of slope-soaring and thermal soaring for travel. Unlike the other seasons, however, birds did not respond navigationally to any of the weather features. Observations of residents and migrants in Costa Rica (Ferland-Raymond *et al.,* 2005) suggests that residents tend to fly low over the forest canopy searching for carrion, whereasmigrants fly higher over the canopy, presumably in more stable air. This contrast in flight behavior between migratory and non-migratory individuals in the tropics suggests that during winter, birds are navigating based primarily on foraging, and are less likely to navigate based on a search for stable air. This interpretation is reinforced by the importance of TKE in the navigation models for all seasons but winter.

We show a strong link between movement patterns and their underlying processes based on responses to external stimuli. By building strong links between ecology and regional scale meteorological models, we show that turkey vultures respond differently to winds, turbulence, and terrain ruggedness based on the time of year and their underlying biological motivations. These different responses lead to significantly different movement patterns, in activity throughout the period, in terms of turning angles, and

distances. We further used these different processes to support various hypotheses of movement: energy-minimization for fall migration, some combination of energy- and time-minimization for spring migration, and a lack of response to weather conditions in route choice during the breeding-period. We feel that there is a strong role for similar inferential techniques in understanding the movement of other animals.

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Conclusion

In this dissertation, we looked at a range of movements, movement decisions, and environmental conditions. These studies included individual choice experiments, observations of behavioural change under novel environmental conditions, tracking migratory paths for a species about which migration was poorly understood, and understanding when and why these migratory paths and the decisions that lead to them might vary across different weather and landscape conditions. In addition, we placed these migratory movements into an annual context by comparing them to breeding and over-wintering movements.

A key focus of this approach involved collecting extensive field observations on individuals, and using these to build individual-based models of movement processes. To do this, we quantified environmental conditions using regional scale atmospheric models, which allow us to understand turbulence, heat flux, winds, and other conditions at the place, time, and altitude where movement decisions are made.

This work makes possible to two critical next steps. Firstly, since movements and behaviors are linked through detailed correlations to regional atmospheric models used in forecasting, changes in movement behavior and changes in movement patterns can be predicted under a range of forecasting scenarios. This would allow educated guesses about what migrations, foraging, home ranges, and population connectivity might look like under a range of possible future climate scenarios. Secondly, it should allow us to understand what conditions are being optimized for during migratory, foraging, and other movements, and to generate predictive models that demonstrate what movement patterns will look like under a range of optimality criteria.